MICROHABITAT USE BY *PODOMYS FLORIDANUS* IN THE HIGH PINE LANDS OF PUTNAM COUNTY, FLORIDA

By

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Abstract of Dissertation Presented to the Graduate School of the University of Florida in Partial Fulfillment of the Requirements for the Degree of Doctor of Philosophy

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By

Cheri A. Jones

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Chairman: John F. Eisenberg
Major Department: Zoology

The purpose of this project was to examine the use of tortoise burrows (Gopherus polyphemus) by the Florida mouse (Podomys floridanus) in high pine (longleaf pine sandhills) on the Katharine Ordway Preserve/Swisher Memorial Sanctuary in Putnam County, Florida. Mark-and-recapture techniques were used at tortoise burrows and on grids (10000 m^2) in order to describe burrow use by mice and to measure home ranges. I also performed a food supplementation experiment to test the hypothesis that population sizes were food-limited. Finally, I examined how local distributions of Florida mice were correlated with vegetation structure and affected by prescribed burns.

Podomys floridanus are commensals of Gopherus in high pine habitats at Ordway, as indicated by trapping success, escape responses, burrow excavations, and observations of

mice in the field. In five years of trapping at burrows on a single sandhill, 255 mice were marked. Of this total, 32% were captured only once and 8.6% survived for 360-920 days. Reproductive activity was concentrated in August, September, and October. Florida mice appeared to be opportunistic feeders, accepting a wide variety of fruits, seeds, and insects. Populations appeared to be limited by factors other than food. Mean annual home ranges were 2601 m^2 for adult females, whose ranges were mutually exclusive. Home ranges of adult males were significantly larger (4042 m^2) and overlapped with those of other adults. Numbers of captures at burrows were best correlated with large numbers of herbaceous species and high stem counts of Pinus palustris, Quercus laevis, and Diospyros virginiana; there was little correlation with ground cover characteristics. Immediate responses of Podomys to prescribed burns were not spectacular, but in the long term, populations appeared to be more stable on sites that were burned periodically than on areas not burned. Implications for conservation of Podomys on the Ordway Preserve also were discussed.

INTRODUCTION

An understanding of home range, diet, burrow use, and other interactions between an animal and its physical environment is crucial for the management and conservation of threatened and endangered species. However, little is known about the ecology of Florida's only endemic mammal, the Florida or gopher mouse. This mouse, Podomys floridanus (Rodentia: Muridae), is listed as Threatened by the Florida Committee on Rare and Endangered Plants and Animals (Layne, 1978) and as a Species of Special Concern by the Florida Game and Fresh Water Fish Commission (1987). Podomys floridanus lives in a narrow range of habitats; my study, and those by Layne at the Archbold Biological Station in Highlands County, suggest that P. floridanus populations are higher in the southern sand pine scrub than in the high pine lands (also known as turkey oak-longleaf pine sandhills or high pine hills). The special listing of P. floridanus is due to destruction of high pine and scrub habitats and to the decline of gopher tortoise (Gopherus polyphemus) populations. Nash (1895) stated that high pine was the most extensive of the five habitats he recognized in Florida; by

1982 approximately 57% of this habitat had been lost (Auffenberg and Franz, 1982).

In the high pine lands of northern Florida, the Florida mouse is associated closely with burrows of the gopher tortoise (Blair and Kilby, 1936; Humphrey et al., 1985; Brand, 1987). My preliminary field studies showed that populations of Florida mice were relatively high and stable on certain sandhills, whereas populations fluctuated to a greater degree on other sites. I was intrigued by the differences I observed in these populations. How did these sandhills differ from each other? Why were certain tortoise burrows favored nesting sites, year after year, whereas other burrows never were used? In an attempt to determine microhabitat preferences in the high pine habitats, I tried five approaches:

1) Do Podomys in the high pine depend exclusively on tortoise burrows? Mouse-use of tortoise burrows was monitored over a five-year period so that long-term "burrow histories" could be constructed.

2) How large are home ranges in the high pine? Home range areas of Podomys in high pine were measured.

3) Do dietary data explain why some tortoise burrows are preferred over others? Diets of these mice were observed in the field and laboratory. A supplemental feeding experiment was performed to test the hypothesis that population size is food-limited (i.e., does increased food supply produce an increase in numbers and body size of mice and an increase in the length of the breeding season?).

4) Is the local distribution of these mice predictable? Physical parameters of burrows, and the vegetation surrounding them, were quantified.

5) Do populations respond positively to burns? Effects of prescribed burns on populations of *Podomys* were determined.

TAXONOMY AND SYSTEMATICS

Podomys floridanus is the only mammalian species endemic to Florida. The species was described as *Hesperomys floridanus* by Frank Chapman in 1889, with the type locality in Gainesville, Alachua County.

Podomys floridanus has long been recognized as distinct from North American species of *Peromyscus*. Osgood (1909) considered *Podomys* a distinct subgenus within the genus *Peromyscus*. Apparently Hooper (1958) was the first to suggest that the closest relatives of *Podomys* were not the cotton mouse and other local *Peromyscus*, but peromyscines in Central America. In Carleton's (1980) major revision of the genus *Peromyscus*, *Podomys* was raised from subgenus to genus. Carleton suggested that *Podomys* shared a common ancestor with *Habromys* and *Neotomodon* from Mexico and Guatemala; these three genera grouped together consistently in his cladistic analysis of 79 morphological characters.

The proposed affinity between *Podomys* and mice from Central America is supported by three lines of evidence:

1) Reproductive tract. The baculum of *Podomys* is relatively small and slender, compared to that of northern *Peromyscus*. Linzey and Layne (1969) examined additional features of the male reproductive tract and noted reduced vesicular and

prostate glands, enlarged ampullary glands, and other features that suggested affinity with Habromys.

2) Ectoparasites. The "typical and only common flea" of Podomys, described by Johnson and Layne (1961), is Polygenis floridanus, which most closely resembles a species found in South America. According to Wenzel and Tipton (1966: 718), "Polygenis is an "expanding" South American genus which has, quite clearly, dispersed into Middle America along with complex-penis-type Cricetinae and caviomorph rodents from South America".

3) Electrophoresis. In their analysis of genic variation among Peromyscus, Smith et al. (1973) considered Podomys one of the least variable species of the group. One possible explanation for this low variability is the maintenance of low numbers in a relictual population.

The fossil record of the Florida mouse is limited to six Rancholabrean assemblages in this state, so there is not much light shed on the distribution of Podomys prior to the Illinoisan. However, a western affinity might be indicated by a Pleistocene species (Peromyscus oklahomensis) from the Illinoisan and Sangamonian of Oklahoma and Texas, that might be related to Podomys (Stephens, 1960). Unfortunately, only a few isolated teeth of this extinct species have been found.

Podomys is not unique among the flora and fauna of Florida in its apparent affinity to Central America. Several plants (such as Opuntia, the prickly pear) and several reptiles, birds, and mammals are considered species of western affinity. Some, such as Gopherus polyphemus, show a disjunct distribution (Blair, 1958). Among the mammals, Webb and Wilkins (1984) found that 15-28% of the mammals from

five Pleistocene sites in Florida were neotropical species. They suggested that the arrival of most of these species could be explained by a Gulf Coastal Corridor, which served as a pathway for southern and western immigrants in the early Pleistocene.

DISTRIBUTION

In recent times P. floridanus occurred from St. Johns, Clay, Alachua, Putnam, Suwannee, and Taylor counties south to Sarasota, Highlands, and Dade counties, with isolated populations in Franklin County and on Merritt Island (Osgood, 1909; Layne, 1978; Stout et al., 1979). A survey of the present distribution of Podomys is urgently needed.

Podomys is the characteristic mouse of some of the most xeric habitats in Florida. It is most common in sand pine scrub and high pine, although it also is found in slash pine-turkey oak and coastal strand associations (Bangs, 1898; Layne, 1978; U.S. Dept. Agric., 1980). On Fig. 1, I have mapped the distribution of scrub and high pine, as indicated by the Soil Conservation Service (U.S. Dept. Agric., 1980), and localities from which Podomys have been reported (Layne, 1978). Clearly there is a close association between Podomys and these two habitats. Layne (in press) has suggested that the scrub was the ancestral home of this mouse, with the high pine a secondary habitat.

In some areas, P. floridanus and P. gossypinus appear to coexist (Layne, 1970). In Putnam County, however, trapping by Suzanne Brand (1987), John Eisenberg (1983; 1988),

Fig. 1. Distribution of Podomys floridanus (triangle designates type locality). Stippling represents distribution of high pine and scrub habitats.

Eric Milstrey (1987), and me has indicated a clear separation between these two species, with P. gossypinus occurring only in lower, wetter microhabitats, and Podomys only in sandhills, or along edges between sandhills and old pastures or sandhills and xeric hammocks.

MATERIALS AND METHODS

I conducted this research on the Katharine Ordway Preserve-Carl S. Swisher Memorial Sanctuary, located about 4 km E of Melrose in Putnam County. The preserve, 37 km^2 in size, is administered jointly by the Florida Museum of Natural History, the University of Florida's School of Forest Resources and Conservation, and the Nature Conservancy.

Approximately one-third of the Ordway Preserve is covered by high pine land (*sensu* Nash, 1895). This habitat is characterized by an open canopy of longleaf pine (*Pinus palustris*) and turkey oak (*Quercus laevis*), although other trees, including sand pine (*P. clausa*), Chapman's oak (*Q. chapmanii*), and bluejack (*Q. incana*), also are present. The understory consists of scattered shrubs, and herbs and grasses. On Ordway the characteristic grass of the high pine land is wiregrass (*Aristida stricta*); other common grasses include pineywoods dropseed (*Sporobolus junceus*), six species of bluestem (*Andropogon* spp.), and three species of threeawn (*Aristida* spp.). Additional grasses identified on the preserve are included in the list compiled by David W. Hall and Richard Franz (unpubl. data). Reindeer moss

(Cladonia and Cladina spp.) is common. The herbs I identified on my study sites are listed in the Appendix.

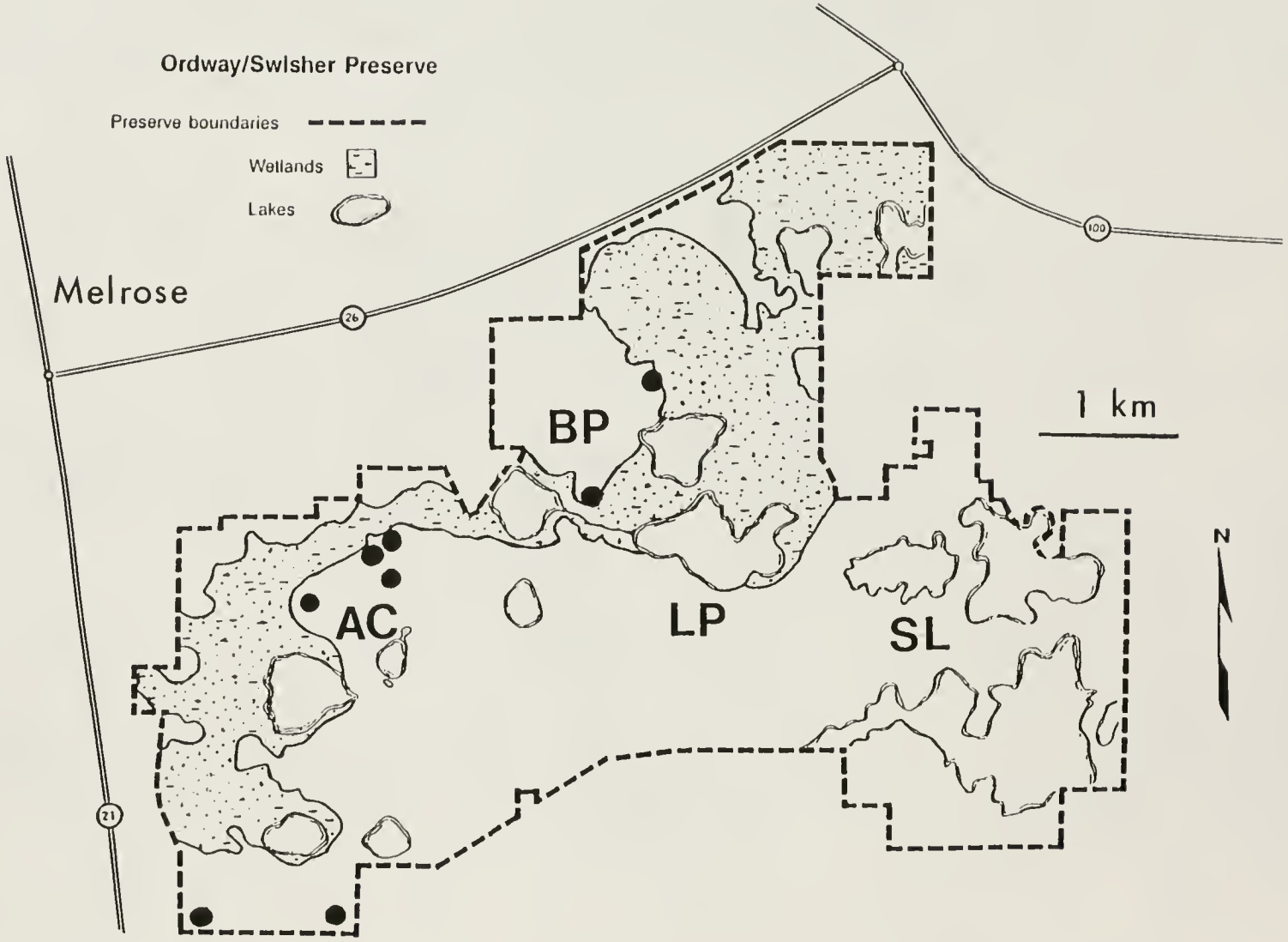
The soils of high pine are sandy and well-drained. There are many patches of bare ground, which become covered with oak leaves, pine needles, tree branches, and other debris in the absence of fire. Under the pines, the needle litter is several inches deep; in areas where the turkey oaks predominate, leaf litter is distributed unevenly by the wind. Burrows of the gopher tortoise (Gopherus polyphemus) are prominent features on this landscape, although population densities probably were higher in coastal areas before human development (Carr, 1940; Auffenberg and Franz, 1982; Cox et al., 1987).

Other mammals found on the high pine land are the opossum (Didelphis virginianus), pocket gopher (Geomys pinetis), fox squirrel (Sciurus niger), flying squirrel (Glaucomys volans), armadillo (Dasypus novemcinctus), raccoon (Procyon lotor), and white-tailed deer (Odocoileus virginianus). Eisenberg (1988) and Franz (1989) compiled lists of mammals known from the various habitats of Ordway. Carr (1940) listed the amphibians and reptiles of high pine habitats. On my study sites, I saw gopher frogs (Rana areolata), oak toads (Bufo quercicus), fence lizards (Sceloporus undulatus), six-lined racerunners (Cnemidophorus sexlineatus), pine snakes (Pituophis melanoleucus), crowned snakes (Tantilla spp.), southern black racers (Coluber

constrictor), coachwhips (Masticophis flagellum), coral snakes (Micrurus fulvius), pigmy rattlesnakes (Sistrurus miliarius), eastern diamondbacks (Crotalus adamanteus), and tortoises (G. polyphemus). Birds common to high pine were listed by Nelson (1952), who thought the avifauna of the high pine did not differ substantially from those of oak hammocks and other nearby communities. However, Maehr et al. (1982) suggested that the high pine might support a greater density of birds than flatwoods and xeric hammocks. I did not attempt to identify birds on my study sites in detail.

On the Ordway Preserve, all locations at which P. floridanus have been found are in high pine habitats, or at the ecotone between high pine and hammock or high pine and old pasture (Brand, 1987; Eisenberg, 1988) (Fig. 2). I trapped mice on four independent high-pine sites, designated Anderson-Cue (AC), Blue Pond (BP), Longleaf Pine Pasture (LP), and Smith Lake (SL). The history of fire on these sites is described below in the Prescribed Burns section. Smith Lake is my longterm study site; Eisenberg and Franz started research projects there in 1983, marking tortoise burrows and trapping Florida mice, gopher frogs, and other burrow inhabitants. I trapped mice at SL from 1984 through 1988. SL is approximately 16.8 ha in size. Vegetation consists of P. palustris, Q. laevis, Q. chapmanii, Q. geminata, and grasses and forbs characteristic of the high pine.

Fig. 2. Distribution of Podomys on the Ordway/Swisher Preserve. Locations of Anderson-Cue (AC), Blue Pond (BP), Longleaf Pine (LP), and Smith Lake (SL) are shown. Dots represent additional locations where Podomys have been captured.


Ordway/Swisher Preserve
Preserve boundaries
Wetlands
Lakes
Melrose
26
100
21
BP
AC
LP
SL
1 km
N

The Anderson-Cue sandhill is the highest in elevation of the four sites; typical vegetation there includes P. palustris and Q. laevis, with fewer Q. geminata than on SL. I worked there from 1986 to 1988. AC was burned in the winters of 1983, 1986, and 1989. It was not included in my study of prescribed burns because I did no pre-burn trapping there. The Longleaf Pine Pasture Sandhill is south of the pine pasture surrounding the old Swisher Estate (Fig. 2). Part of this sandhill, the most disturbed of my study areas, has been planted in slash pine. Dominant plants here include maidencane (Panicum hemitomon) and centipede grass (Eremochloa ophiuroides), which are not typical of natural high pine vegetation. There are many turkey oaks and several large patches of gopher apple, but fewer longleaf pines, pawpaws, and other high pine species. I worked on LP for only one trapping season for the purpose of gathering additional information regarding prescribed burns. The fourth study site, Blue Pond, was logged intensively. There are few longleaf pines, and turkey oaks are by far the most numerous trees. Ground cover is sparse in some areas but rather dense in others. Species composition of the ground cover appeared similar to that of SL.

As described in the following chapters, I trapped P. floridanus at tortoise burrows and on grids using standard mark-and-recapture techniques (Davis, 1956). While trapping at burrows, I numbered, marked, and mapped each burrow, and

then placed a pair of Sherman traps (baited with oatmeal) at the entrance, or just inside the mouth, of the burrow. Animals were marked by toe-clipping and then weighed. I also noted sex, reproductive condition, and presence of ectoparasites. Animals were released near the burrow entrance, and in most cases I recorded whether they entered the burrow or ran elsewhere. I collected the same data on grids. I placed one grid (designated SL) on my study site on the south side of SL; two more grids (ACI and ACII) were set north and east of the Anderson-Cue ponds. Grids were more than 100 m apart to reduce movement of animals between grids. Each grid consisted of 10 columns and 10 rows 10 m apart (area = 10000 m^2), with a single Sherman at each intersection. Each tortoise burrow and grid location was given a unique number and marked with forestry flags. On the burrow flags I also attached an aluminum tag (Al Tag, Forestry Suppliers, 205 W. Rankin Street, Jackson, Mississippi 39204) bearing the burrow number. These tags survived all but the hottest burns, thus serving as more permanent markers of burrow locations.

Traps were opened near sundown and checked at or shortly following sunrise. Because of temperature extremes, morning condensation, and (in some months) heavy rain, I found it necessary to check traps in the morning as quickly as possible. Animals developed hypothermia when ambient temperatures reached 10 C; I extended the trapping season

into November by insulating traps with a handful of excelsior, wood shavings used in packing glassware. Mice compress the excelsior into a pad on top of the treadle. Spanish moss also can be used, but I found the wood to be superior because it does not absorb moisture. I did not trap in December or January; fieldwork resumed when warm weather resumed (February-April).

I measured trapping effort as trapnights (one trapnight being one trap/night). Results of the vegetation analyses were run on SYSTAT at the IFAS Consulting Center at the University of Florida; other statistics were performed on a hand-held calculator. Statistical methods are described in each chapter.

USE OF TORTOISE BURROWS

Dependence on Burrows

Previous students of peromyscine behavior and morphology concluded that Podomys was primarily a terrestrial species; although capable of climbing and digging, Podomys climbed and dug less than several species of Peromyscus to which it was compared (King, 1968; Layne 1970; Layne and Ehrhart, 1970; Siegel and Van Meter, 1973). In some areas, these mice seemed capable of excavating their own burrows; Lee (1968) stated that P. floridanus built burrows greater than 120 cm in depth in scrub habitats, and Starner (1956) trapped one animal in a small burrow that she thought might have been dug by the mouse (in the ecotone between the mesic hammock and longleaf pine flatwoods at San Felasco Hammock, Alachua County). Layne and Ehrhart (1970) suggested that Podomys rarely dug its own burrows, but Layne (in press) noted high populations of Florida mice in scrubs where tortoises were absent or occurred in low numbers. However, observations by Eisenberg (1983), Brand (1987), and myself suggested a much closer relationship between Podomys and Gopherus in the high pine in Putnam County.

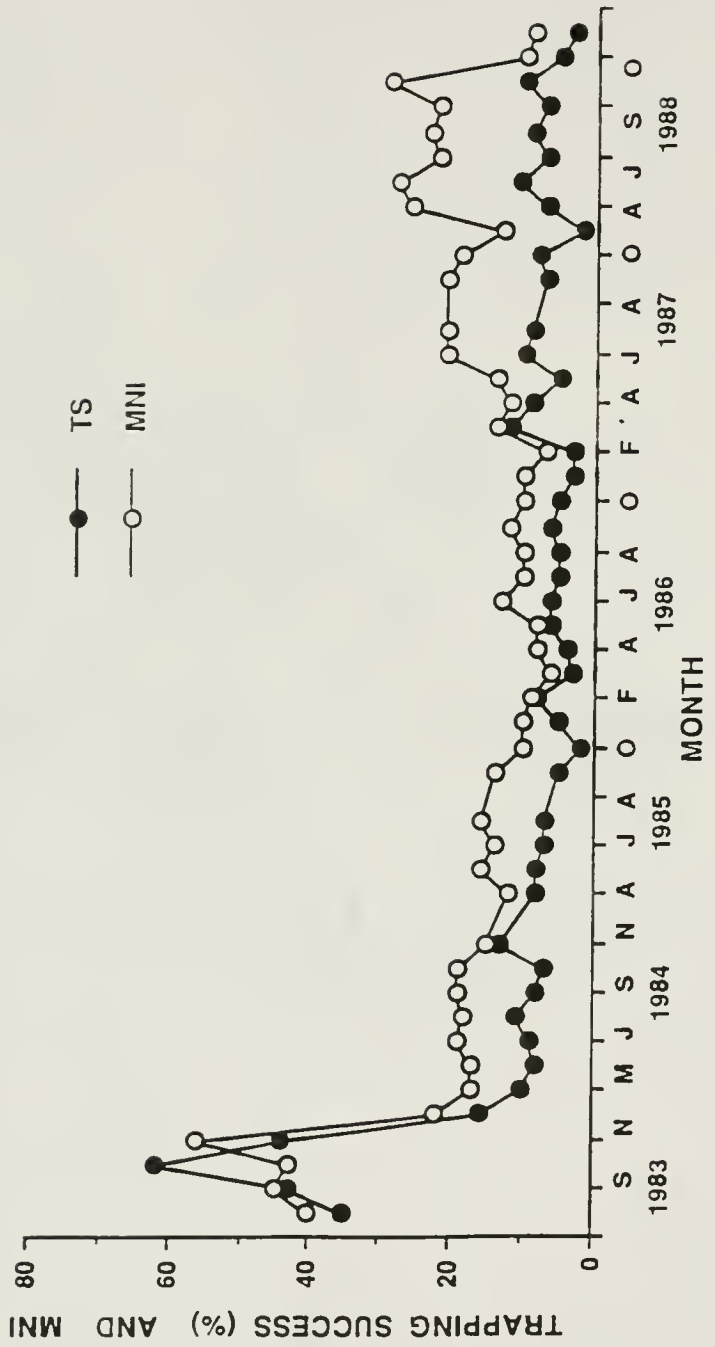
Blair and Kilby (1936) were the first to note in the literature that Podomys floridanus used burrows of Gopherus polyphemus in northern and central Florida. They saw mice using active burrows (i.e., burrows that had tortoises in them) in an old field in Alachua County. Three of the 15 mice captured by Starner (1956) were taken from traps placed inside entrances of tortoise burrows. Milstrey (1987:115) reported that "Florida mice were continuously present" in many tortoise burrows at his study site in Putnam County. Johnson and Layne (1961) also noted that Podomys inhabited tortoise burrows, and possibly burrows of pocket gophers (Geomys pinetis). At other sites Podomys used burrows constructed by Peromyscus polionotus, Sigmodon hispidus, G. pinetis, and Dasypus novemcinctus (Gentry and Smith, 1968; Layne, in press). However, in my 33,385 trapnights on burrows and grids at Ordway I have observed Florida mice entering small holes of unknown origin only three times (twice on SL and once on AC), and I have no evidence that they inhabited logs or other shelters.

I found that mice almost always ran down tortoise burrows when released. For example, I tallied escape responses of 18 Podomys caught on the AC grid (and therefore released at grid coordinates, not at burrows). Out of 35 captures, mice ran down tortoise burrows 25 times; they hid in the base of turkey oaks or in fallen logs and other debris 10 times. In my regular trapping sessions, I never

saw mice climb vegetation as an escape response; Eisenberg (pers. comm.) noted one such response in 1989. However, my field observations have confirmed climbing ability by these mice (Jones, 1989, and Home Range below). In T-maze tests of arboreality performed by C. A. Langtimm at SL (in which a T-maze was propped against an oak), most mice jumped off the T, but the animals who chose to climb oaks reached heights of 8 m (C. A. Langtimm, unpubl. data). Clearly these animals are capable of climbing, even though the time spent on this activity in any one night remains unknown.

In preliminary studies on the Ordway Preserve, Eisenberg (1983) reported that trapping success was much higher if traps were placed at the mouths of tortoise burrows (33%) than on transects (0.4%). Humphrey et al. (1985) caught 113 mice in 1,144 trapnights at 51 burrows, also at Ordway. In 146 trapnights on transects--in which traps were not placed at burrows--I caught no mice. At the SL burrows in August, September, October, and November 1983, Eisenberg (unpubl. data) had trapping successes of 35, 43, 62, and 44%, respectively. I calculated trapping success using adjusted trapnights, which indicated how many traps were available after subtracting half the number of traps sprung and containing non-target species from the total number of traps set. My trap success for Podomys ranged from 0 to 16%, with SL being the most successful (2-16% with a mean of 7%) (Fig. 3). Variations in total trapnights (within and among sites)

Fig. 3. Trapping success (%) and minimum numbers of individuals (MNI) (adults and subadults) of Podomys at burrows on the Smith Lake Sandhill. Monthly trapping effort was unequal among months.


TS
MNI
TRAPPING SUCCESS (%) AND MNI
0
20
40
60
80
S N M J S N A J A O F A J A O F A J A O S O
1983
1984
1985
1986
1987
1988
MONTH

reflect my attempt to maximize sample size by trapping at all tortoise burrows on each sandhill until burrows disappeared.

On all four sandhills, traps at burrows occasionally were sprung by falling branches or by insects removing bait. A large number of sprung traps was an occasional problem at AC, but a more major one at BP, particularly on the north side. There I identified tracks of armadillos, raccoons, and dogs, but I suspected dogs were the major culprits. One morning I found two traps covered with urine and several times I saw dogs on the sandhill, which was the closest of my sites to the periphery of the preserve. It is also worth noting that I found more carcasses of turtles and tortoises here than on any other study site. Following a suggestion of M. E. Sunquist, I fashioned "croquet hoops" out of aluminum welding rods and placed them around the traps. They helped decrease the number of traps moved, but did not always prevent closing of trap doors.

In traps at burrows, the most frequently-captured non-target species was Rana areolata (Table 1). At SL, from September 1984 to the end of the study, gopher frogs were captured 105 times. Other occasional captures were camel crickets (Ceuthophilus sp.), centipedes, southern toads (Bufo terrestris, once on AC, LP, and SL), six-lined race-runners (Cnemidophorus sexlineatus), and a young rabbit (presumably Sylvilagus floridanus, on SL). All of these

TABLE 1. Numbers of captures of non-target species in traps at burrows (22,085 trapnights) and on grids (11,300 trapnights). Captures of insects and centipedes were not counted. Scientific names are listed in text.

Burrows	Grids
camel crickets	grasshoppers
1 spider	cockroaches
3 southern toad	centipedes
129 gopher frog	3 six-lined racerunner
3 six-lined racerunner	2 fence lizard
1 cotton mouse	1 black racer
38 flying squirrel	2 rice rat
1 rabbit	3 cotton rat
	148 flying squirrel

species are known to use Gopherus burrows (Jackson and Milstrey, 1989). In 1988 I began catching flying squirrels (Glaucomys volans) at the AC and SL burrows; at SL I captured squirrels 27 times from May to October, 15 times in May alone. These results must indicate some change in the Glaucomys population that resulted in additional terrestrial foraging, or perhaps they reflect learned behavior of animals who found oats at traps on grids. At any rate, I observed only one flying squirrel enter a burrow upon release, and I do not believe they reside in tortoise burrows on these sandhills.

At study sites other than Ordway, additional murids, including P. gossypinus and P. polionotus, visit tortoise burrows (Jackson and Milstrey, 1989). In 22,085 trapnights at burrows on the AC,BP, LP, and SL sandhills I caught only one cotton mouse (P. gossypinus, on AC). In other Ordway studies, Eisenberg (1983) and Brand (1987) found Podomys in the high pine and Peromyscus in the hammocks and flatwoods. Clearly, Podomys is the only rodent that regularly inhabits tortoise burrows in these sandhills. At burrows in other Ordway habitats, the absence or lower numbers of Podomys might represent a case of competitive exclusion; after the 1987 drought Eisenberg (pers. comm.) reported trapping Florida mice in hammocks closer to lakes than in previous years, and Peromyscus were absent.

For comparative purposes, trapping results on two grids on AC and one grid on SL also are shown (Fig. 4). Trapping success on grids ranged from 0 to 7% (AC) and from 0 to 6% (SL); mean trapping successes were 0.47%, 0.70%, and 3.6% for ACI, ACII, and SL. Traps on grids were more likely to be sprung by rain, falling branches, pine cones, and raccoons than were traps at burrows. Only one Florida mouse (female 18, a juvenile known to be alive 36 days at SL) was found on a grid and not during burrow trapping. Flying squirrels were caught more frequently (Table 1), usually at traps near the bases of pines, oaks, or dead trees. One cotton rat (Sigmodon hispidus) was captured once at SL; this was a juvenile male (which I marked) presumably dispersing across the high pine. The other cotton rats and the rice rats (Oryzomys palustris) were caught on the AC grids on 28 and 29 June 1988; their appearance on the grids might reflect drought-related dispersal out of the vegetation surrounding the AC ponds. Centipedes occasionally were caught on all grids. On ACI I also captured grasshoppers, cockroaches, fence lizards (Sceloporus undulatus), six-lined racerunners (C. sexlineatus), and a black racer (Coluber constrictor).

Description of Burrows

The size and configuration of tortoise burrows have been described by Hallinan (1923) and Hansen (1964). Blair

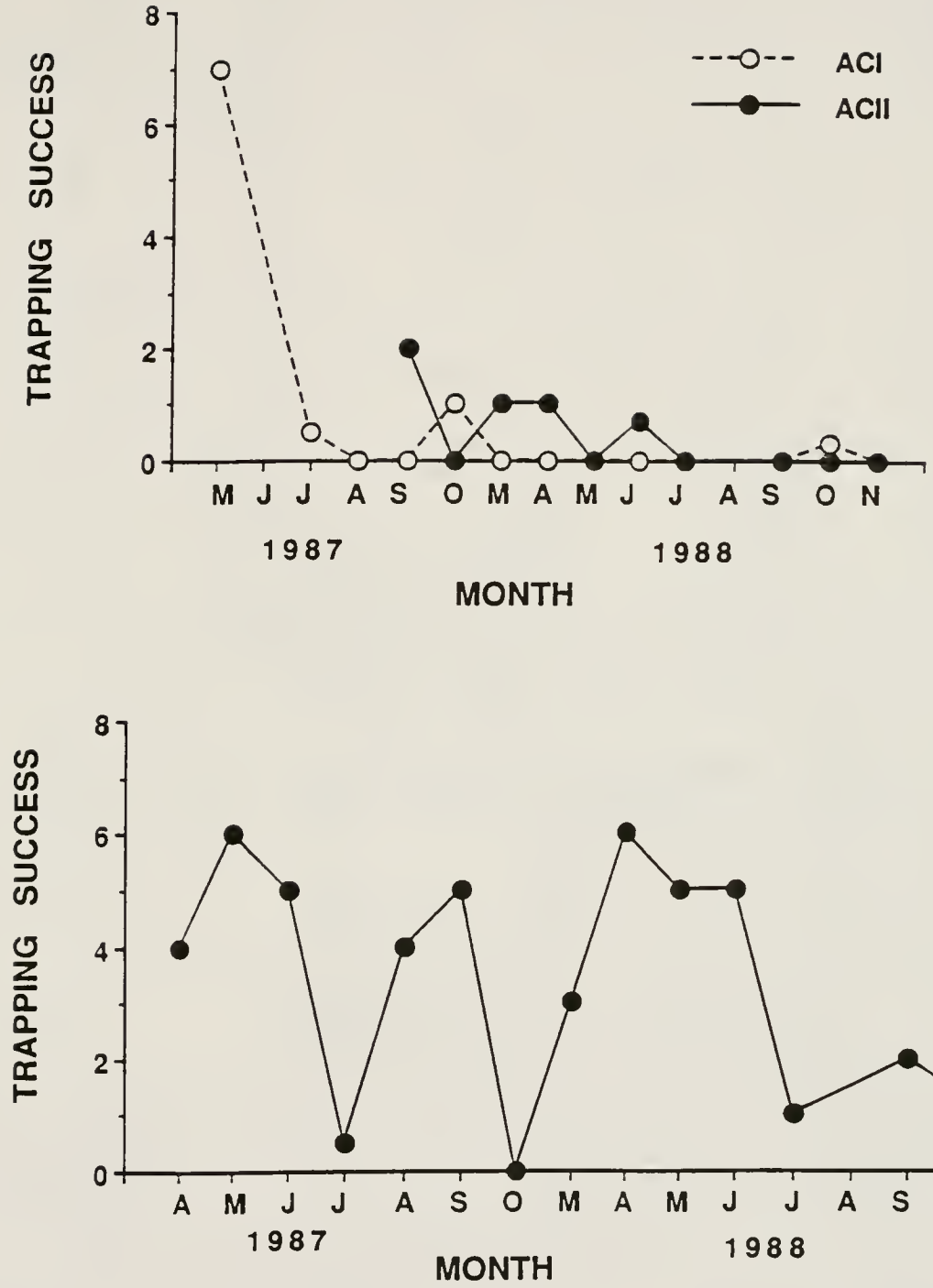


Fig. 4. Trapping success (expressed as the total number of captures/adjusted trapnights) for Podomys on the AC (top) and SL (bottom) grids.

and Kilby (1936) noted the use of a small hole approximately 182 cm from the entrance of a burrow. However, the only description of structures used by Podomys was that of Layne (in press), who described nests, nest chambers, and small tunnels found in two tortoise burrows in Alachua County. Richard Franz and I excavated five burrows on Ordway in order to further describe structures utilized by mice. Typically, mice used small U-shaped tunnels constructed off one side of the tortoise burrow, with both entrances to the U opening into the main burrow. We also noted use of tunnels we dubbed "chimneys", which ran from the ceiling or side of the burrow to an outside opening a meter or two past the main entrance. In all five burrows, mouse activity appeared concentrated in the upper 2 m of the burrow. Additional details of the actual excavations were discussed by Jones and Franz (in prep.). Chimneys allowed occupation of burrows after the main entrance has collapsed, and might serve as escape routes from predators. Although not all burrows have chimneys (at my four study sites from 6.8% (AC) to 26.9% (BP) of the burrows had chimneys), the presence of chimneys is an indicator of past or present occupation of tortoise burrows by Podomys. Exploratory trapping for mice in the sandhills should not omit observation of these small holes.

To determine the pattern of dispersion of tortoise burrows on the SL sandhill, I used methods described by

Brower and Zar (1984). In this procedure, a grid is placed over a map of the study area and numbers of squares containing no burrows, squares containing one burrow, and etc., are counted. I used a grid with squares 35 mm by 35 mm (which corresponds to 1225 m^2 on the map). My SL study site consisted of 93 squares with a mean of 1.46 burrows per square (or 0.11 burrow/m^2). I included all 136 burrows monitored from 1983 through 1988, without consideration of burrow classification or tortoise demography; that is, I considered only burrow locations without burrow size, duration of residence, or other characteristics. The data fit the Poisson distribution, leading to the conclusion that the 136 burrows on SL are randomly distributed (Table 2). Another method to determine whether distribution is random is the X^2 test, for which I obtained a value of 0.547 (not significantly different from random at $p = 0.05$). As a third method, I tried the Morisita's index of dispersion, which is calculated as $I = n\ [(\Sigma X^2-N)/(N(N-1))]$ where n is the number of squares, N is the total number of burrows counted on n squares, and ΣX^2 is the squares of the numbers of burrows per plots for all plots. A value of 1.0 for I indicates random dispersion; value of 0 indicates uniform dispersion. I obtained I = 0.95, which indicates random dispersion. Finally, I calculated the ratio of observed to expected density; I obtained a value of 0.94, which is close to the value of 1.00 which again indicates random distribution

TABLE 2. Data describing distribution of burrows on SL (top) and AC (bottom) with the probabilities expected from the Poisson distribution (with means of 1.5 and 1.7 burrows per square). X indicates number of burrows per square; f(X) indicates the observed frequency; p(X) is the observed probability; and P(X) the expected Poisson probability.

X	f(X)	p(X)	P(X)
0	20	0.215	0.223
1	33	0.354	0.335
2	24	0.258	0.251
3	10	0.108	0.126
4	5	0.054	0.047
5	1	0.011	0.014
0	15	0.259	0.183
1	13	0.224	0.311
2	13	0.224	0.264
3	12	0.207	0.150
4	3	0.052	0.064
5	0	0	0.022
6	0	0	0.006
7	2	0.035	0.001

(Brower and Zar, 1984). The 101 AC burrows also were dispersed randomly (X^2 = 5, significant at p = 0.10; I = 0.98; ratio of observed to expected = 1.29).

Observations of dispersion of other gopher tortoise burrows vary. McRae et al. (1981) and Auffenberg and Franz (1982) recognized burrows clumped as colonies, whereas others reported random distributions (e.g., Kushlan, 1982; Kushlan and Mazzotti, 1984). Whether these discrepancies reflect variations in tortoise behavior or in data collection remains unknown.

Podomys and the Burrow Community

In the high pine, Gopherus burrows provide shelter from the fires and extreme fluctuations in temperature and rainfall that characterize this environment. Burrows of the southeastern pocket gopher (Geomys pinetis) also are common in the high pine, but the two types of burrows are used by different species (Funderburg and Lee, 1968). Eisenberg (1983) suggested that G. polyphemus could be considered a keystone species in the high pine due to the numerous and diverse species that use its burrows. Franz (1986) listed 19 species of amphibians and reptiles that used the SL burrows. The most recent state-wide list of species associated with Gopherus burrows consists of 60 vertebrates (Amphibia, Reptilia, Aves, and Mammalia) and 302 invertebrate species

(Gastropoda, Malacostraca, Arachnida, Chilopoda, Diplopoda, and Insecta) (Jackson and Milstrey, 1989).

Besides using burrows as shelter, I suspect Podomys takes advantage of the invertebrate commensals and visitors. My captive mice readily accepted live crickets and mealworms. Milstrey (1987) described Podomys eating blood and body fluids of engorged ticks (Ornithodoros turicata) that parasitize Gopherus and Rana areolata.

Florida mice are presumably preyed upon by birds, foxes, bobcats, and raccoons (Layne, 1978; Maehr and Brady, 1986; Wassmer et al., 1988). I suspect that in the high pine snakes are major predators, although predation by snakes has not been documented. I occasionally saw coral snakes (M. fulvius) near burrows, but omitted the species from consideration because coral snakes do not prey upon mammals (Jackson and Franz, 1981). Mushinsky (1987) summarized predation records for snakes; some of the species known to take mammals include Coluber constrictor, Drymarchon corais, Elaphe obsoleta, and Pituophis melanoleucus. Several species of snakes utilize tortoise burrows at Ordway and must be considered potential predators of Podomys, including C. constrictor, E. guttata, P. melanoleucus, Masticophis flagellum, D. corais, Sistrurus miliarius, and Crotalus adamanteus (Franz, 1986; Timmerman, 1989). In particular, eastern diamondbacks are known to take Peromyscus, and Timmerman (1989) considered Podomys a potential

prey item. During my time at Ordway, I saw only one diamondback in the high pine (an adult female near BP burrow #319, 6 November 1988). Timmerman (1989) examined habitats used by eight eastern diamondbacks at Ordway from 1985 to 1989. His snakes used high pine and old field habitats less than expected (approximately 13% of all observations) although these two habitats comprised more than 60% of the area available. The diamondbacks spent little time underground, and only 16% of the burrow locations were in Gopherus burrows. However, as Timmerman pointed out, 75% of the locations were in dens of the armadillo, which frequently takes over old Gopherus burrows. Tortoise burrows are used as winter refugia and, in the fall, as parturition sites, leading to the suggestion that Podomys might be important in the diet of young diamondbacks (Timmerman, 1989).

Mortality rates of Podomys due to disease and parasites are unknown. Thirty-two species of endo- and exoparasites of Podomys have been reported (Layne, 1963, 1968a; Lichtenfels, 1970; Whitaker, 1968). Milstrey (1984, 1987) summarized recent studies of the soft tick Ornithodorus, a known carrier of relapsing fever that feeds on residents of gopher burrows, but, as he points out, the relationships between the vertebrates and invertebrates of these burrow systems are still poorly understood.

Life History

I examined demographic data for my largest sample, the 255 P. floridanus marked at the SL burrows, August 1983 to November 1988. Of this total, 52 females and 44 males were marked in 1983. Eighty-one (38 females, 43 males)of the 255 (32%) were captured only once. I calculated minimum trappability ((number of captures - 2)/(possible captures -2)) for animals captured three or more times (Hilborn et al., 1976).

Individual trappability ranged from 14 to 100%. Average trappability was 58% for 27 mice in 1983, 55% for n = 17 in 1984, 58% for n = 16 in 1985, 62% for n = 16 in 1986, 48% for n = 13 in 1987, and 60% for n = 24 in 1988. The average for all five years was 57%. According to Hilborn et al. (1976), when trappability = < 50%, estimates of minimum numbers of individuals (MNI) by direct enumeration will underestimate actual population size; estimates become more reliable as trappability increases. Trappability on grids was lower than on burrows. For example, individual trappability on the SL grid ranges from 38 to 50%.

The reproduction, growth, and development of Podomys were described by Layne (1966). He demonstrated that seasonal distribution of pregnancies in a wild population in Alachua County was bimodal, with the major peak occurring between August and November. At SL, I classified young animals as juveniles if the gray and white juvenile pelage

was still present, and as subadults if the dorsum was gray with gold and agouti hairs appearing along sides and flanks (minimum weights of subadults were approximately 25 g). Numbers of young marked (Fig. 5) and numbers of reproductive adults (Fig. 6) at SL indicate that seasonality of reproduction at Ordway also peaked in the late summer and fall, although juveniles and reproductive adults might appear in small numbers at other times of the year (Layne, 1966).

Juveniles usually were first captured at the mouths of burrows at approximately three weeks of age. At this point the young were still completely gray and white and weighed approximately 9 to 14 g (Layne, 1966). In some cases young appeared at burrows with females (and sometimes males) who were long-term residents, but I had no way of determining parentage of some juveniles and almost all subadults. This, and the fact that many juveniles disappeared before completion of adult molt, suggests that both pre- and post-reproductive dispersal occur.

Captive animals breed year-round (Dice, 1954; Layne, 1966; Drickamer and Vestal, 1973). In captivity mean litter size (1.7-2.6) is slightly smaller than that reported (3.1) for wild-conceived litters (Dice, 1954; Layne, 1966; Rood, 1966; Drickamer and Vestal, 1973; Glazier, 1985). Maternal care in captivity consisted of creating nests, plugging entrances to nest boxes, nursing and grooming young, and herding juveniles into the nest, as described previously by

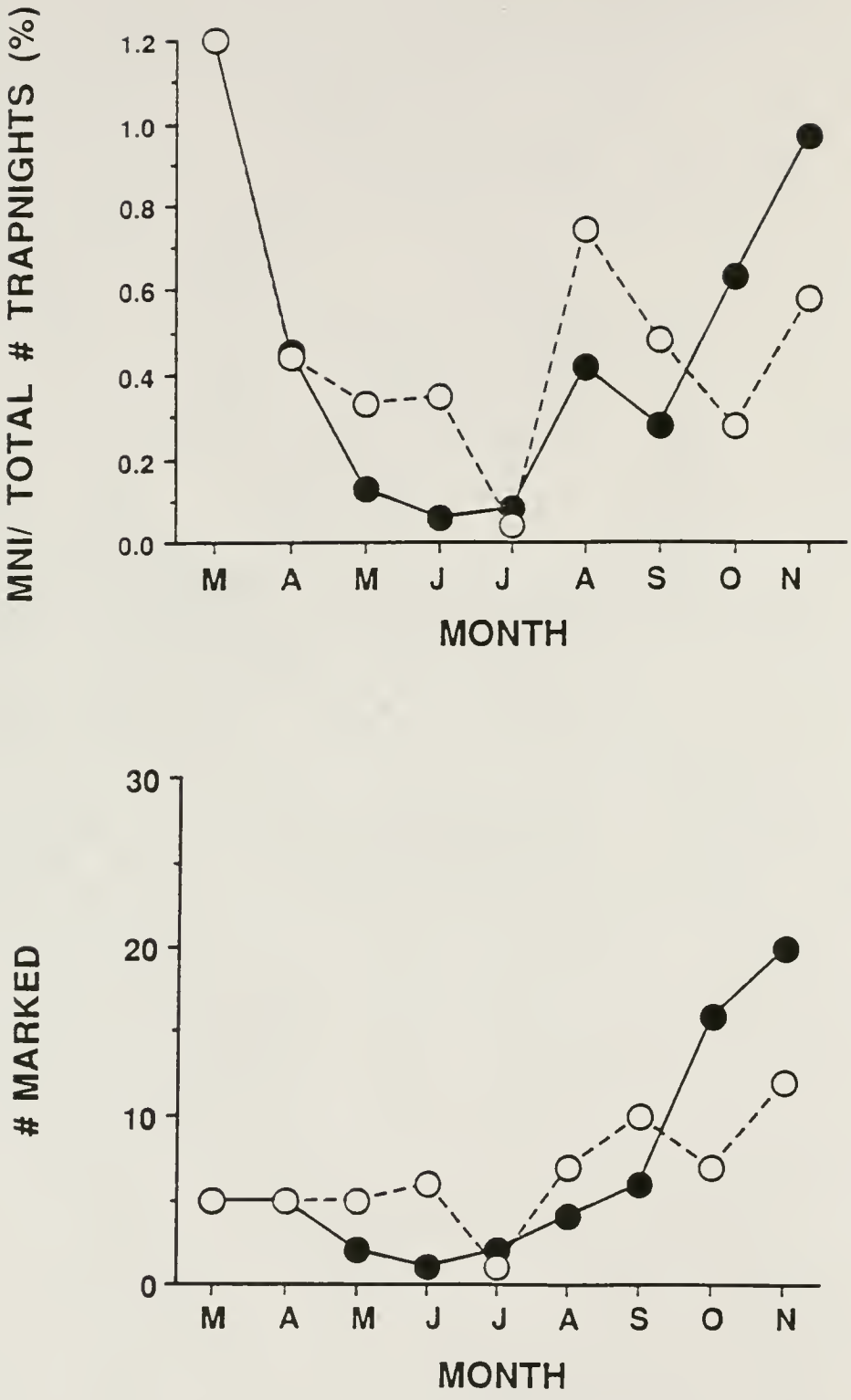


Fig. 5. Numbers of juveniles (dots) and subadults (circles) marked on the SL sandhill, expressed as minimum numbers of individuals/number of trapnights (top) and as numbers of individuals (bottom).

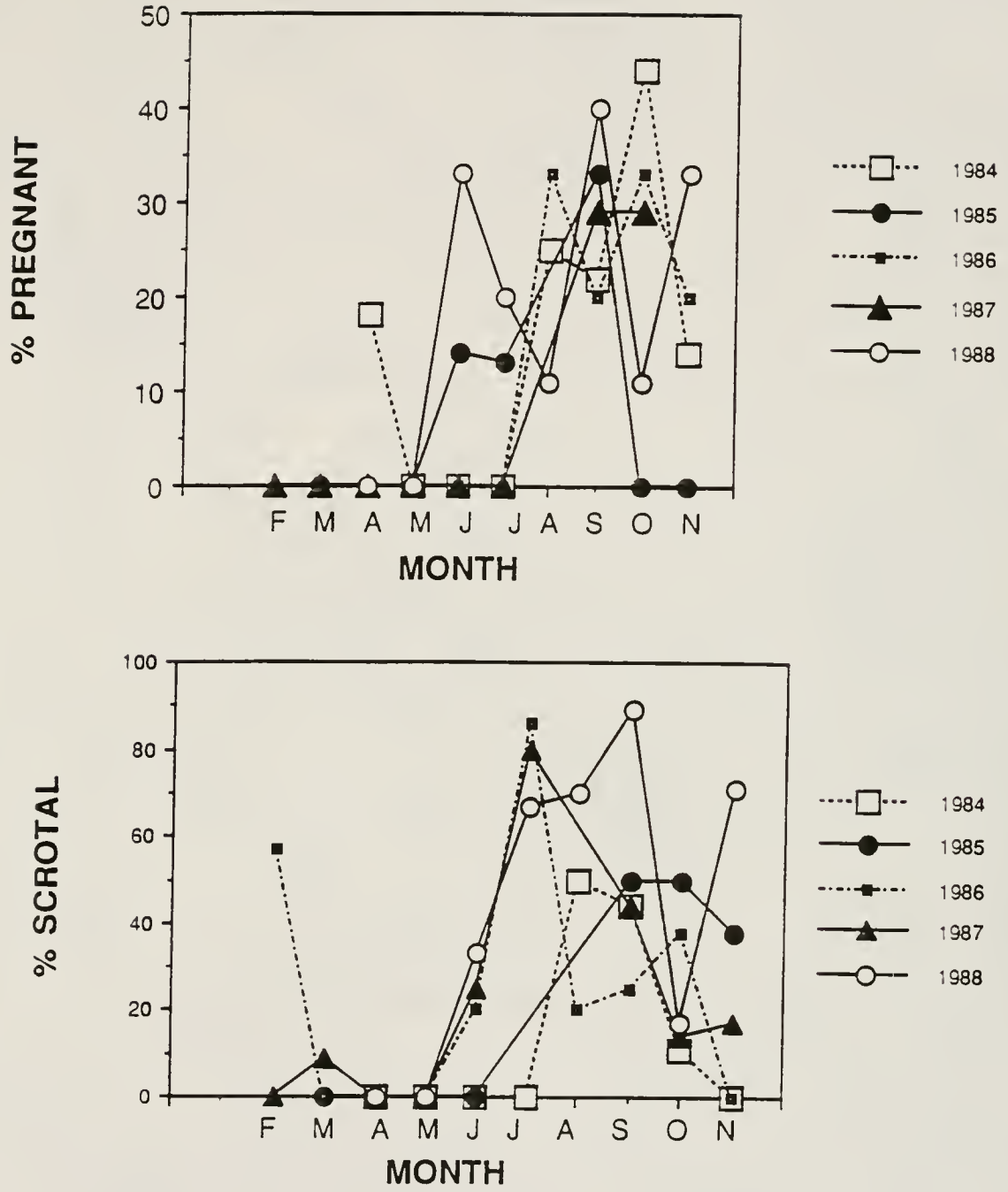


Fig. 6. Reproductive data for Podomys trapped on the SL sandhill, 1983-1988: the proportion of adult females who were pregnant (top) and the proportion of males who were scrotal (bottom) are shown.

Layne (1966, 1968b). In my captive colony 8 females and 5 males produced 54 young in 24 litters; 11 litters were born to a single pair. Litter size ranged from 1 to 4 (mean = 2.25). The distribution of births was: 8 in September; 4 in July; 3 in October; 2 in March, August, and December; 1 in January, February, and November. Four neonates have not been sexed at this time; the remaining young consisted of 24 females, 19 males, and 7 infants who died before gender was recognized.

Longevity of Podomys in the wild is unknown. Keim and Stout (1987) reported that a male captured at approximately three weeks of age lived in captivity for 7 years and 4 months. At SL, 12 females and 10 males (8.6% of the animals marked) were present for more than 360 days (Table 3). Seven females and one male were first marked as juveniles; 20 individuals were first found on the south side of SL and two were marked on the north and later migrated south. In captivity, two- and three-year-olds are continuing to reproduce.

TABLE 3. Longevity records exceeding 360 days for Podomys floridanus at SL. ID is the identification number, YR = year marked, A = age when marked (Juvenile, Subadult, or Adult), and P = persistence (in days) as indicated by both trapping methods. Asterisk indicates trap mortality.

Females				Males			
ID	YR	A	P	ID	YR	A	P
43	83	S	445	39	83	A	905
55	83	J	409	48	83	A	570
65	83	J	649	63	83	S	410
23	84	A	467	11	84	A	920
30	84	A	403	32	84	A	620
61	86	J	360	98	85	A	401*
10	87	J	588	80	86	S	515
19	87	J	385	98B	86	S	500
26	87	J	554	42	87	A	457
47	87	A	547	54	87	J	412
58	87	A	392				
64	87	J	504				

HOME RANGE

The concept of home range most widely accepted by mammalogists is that defined by Burt (1943:351) as "that area traversed by the individual in its normal activities of food gathering, mating, and caring for young. Occasional sallies outside the area . . . should not be considered as in part of the home range. The home range need not cover the same area during the life of the individual." The concept of territoriality, on the other hand, involves domination by either overt or covert social interaction. As defined by Kaufmann (1983:9), a territory is "a fixed portion of an individual's or group's range in which it has priority of access to one or more critical resources over others which have priority elsewhere or at another time."

Among peromyscines, there is considerable variation in descriptions of both home range sizes and degrees of territoriality (Eisenberg, 1968; Stickel, 1968). For P. floridanus, home range and territoriality have not been described. I examined the size of home ranges on the Ordway sandhills with three methods: fluorescent powder, trapping on grids, and trapping at burrows.

Fluorescent Powder

The use of fluorescent powder to track small rodents and to determine movement patterns was introduced in the sandhills of Nebraska (Lemen and Freeman, 1985, 1986). I applied this technique to examine size of nightly activity areas of Podomys on the SL sandhill.

I powdered five animals on 25 May 1985, three on 14 July 1985, and three on 15 June 1987. The first eight animals were trapped at burrows and held until 2100 EST the following evening; the last three were removed from traps on the grid at 0230 EST, powdered, and released immediately. Each animal was placed into a plastic ziplock bag with a fine, nontoxic fluorescent powder (green, pink, or yellow), gently shaken until completely covered, and released at the point of capture. At a later time, I returned with the fluorescent light and marked the powder trails with forestry flags. Trails then were mapped using a tape measure and compass.

The mice showed no ill effects from this technique by loss in weight or other signs of poor condition. One female was so little traumatized by the procedure that she caught and consumed a moth immediately after her release. However, with the exception of the moth incident, I did not obtain additional information regarding feeding.

Powdering was of some use in that it showed animals utilizing fallen trees and branches as runways, as I had

observed in escape responses during trapping. Douglass and Reinert (1982) showed that utilization of fallen logs by Peromyscus leucopus was not an artifact of trapping but part of the animals' normal movements. Additional evidence of climbing was indicated by the powder trail of an adult male (#39), which extended 36 cm up a turkey oak snag.

The powder indicated only one case of social interaction. On 15 June 1987 females 10 and 47 were caught in the same trap. Female 47 was powdered, released, and recaptured later that morning. Again, she was found in the same trap with #10, who also had become covered with powder. Female 47 was first marked as an adult on the SL grid on 19 April; she remained at the grid and surrounding burrows until at least October 1988. Number 10 was a younger female marked as a juvenile on 12 April at a burrow located on the grid; by September she had moved to an area west of the grid. Possibly #10 was a daughter of #47. Use of radioisotopes, DNA fingerprinting, and other techniques would be more appropriate and efficient methods to examine family relationships and dispersal of young Podomys.

Distances traveled by mice, as indicated by powder trails, are shown in Table 4. Trails for two animals were very short (< 10 m), but I believed that a single night's excursion exceeded 10 m. By trapping on 14 July 1985 and 15 June 1987, I discovered powdered mice at locations to which no powder trails led. Thus, the powder trail showed only a

TABLE 4. Activity data from ten Podomys dusted with fluorescent powder at SL. ID indicates sex and identification number of mouse; R indicates the burrow or grid station at which an animal was caught and released; ORI indicates initial direction from release point (in degrees); DIST is the greatest distance (in meters) from R as indicated by fluorescent powder; DEST is the burrow or grid station at which an animal was found the following morning. The actual distance from R to DEST is shown in parentheses.

ID	DATE	R	ORI	DIST	DEST
F23	25 May 85	35	222	5.5	-
F30	25 May 85	13	125	11.9	-
"	14 Jul 85	81	302	9.9	71 (36.0)
F39	25 May 85	58	70	17.7	-
F47	15 Jun 87	6,2	47	20.0	6,0
M11	25 May 85	10	162	15.2	10
M32	14 Jul 85	81	140	28.0	15 (45.0)
M39	14 Jul 85	22	108	19.2	23 (15.0)
M49	15 Jun 85	9,4	273	2.0	9,5 (10.0)
M54	15 Jun 85	9,1	250	15.0	-
M98	25 May 85	49	281	11.5	-

part of the night's activities. Because the fluorescent powder yielded so little information regarding home range, feeding behavior, or social activity, I concluded that it was of little use with Podomys at Ordway.

Trapping on Grids

Results of trapping on the three grids are shown on Fig. 7, which includes data from all animals, including transients caught only once or twice. A total of 18 animals was trapped on the AC grids. I calculated persistence on the grid (P_G) as the number of days from first to last capture. Time spent by each individual on the grid is represented by the horizontal bars; counting bars vertically indicates the size of the known population per month. The largest population occurred on the SL grid in the spring of 1987 and 1988, when there were 8 individuals or 8 animals/ha. Excluding animals caught three times or less, mean persistence time on this grid was 195.9 days for females and 137.2 days for males.

For 20 mice captured four or more times, I plotted the capture locations and number of captures. To calculate the home range area, I used the Exclusive Boundary Strip Method (Stickel, 1954), in which I mapped the capture sites and drew a boundary strip (equal to half the distance between traps). I selected this approach because Stickel (1954) compared the exclusive boundary strip, inclusive boundary

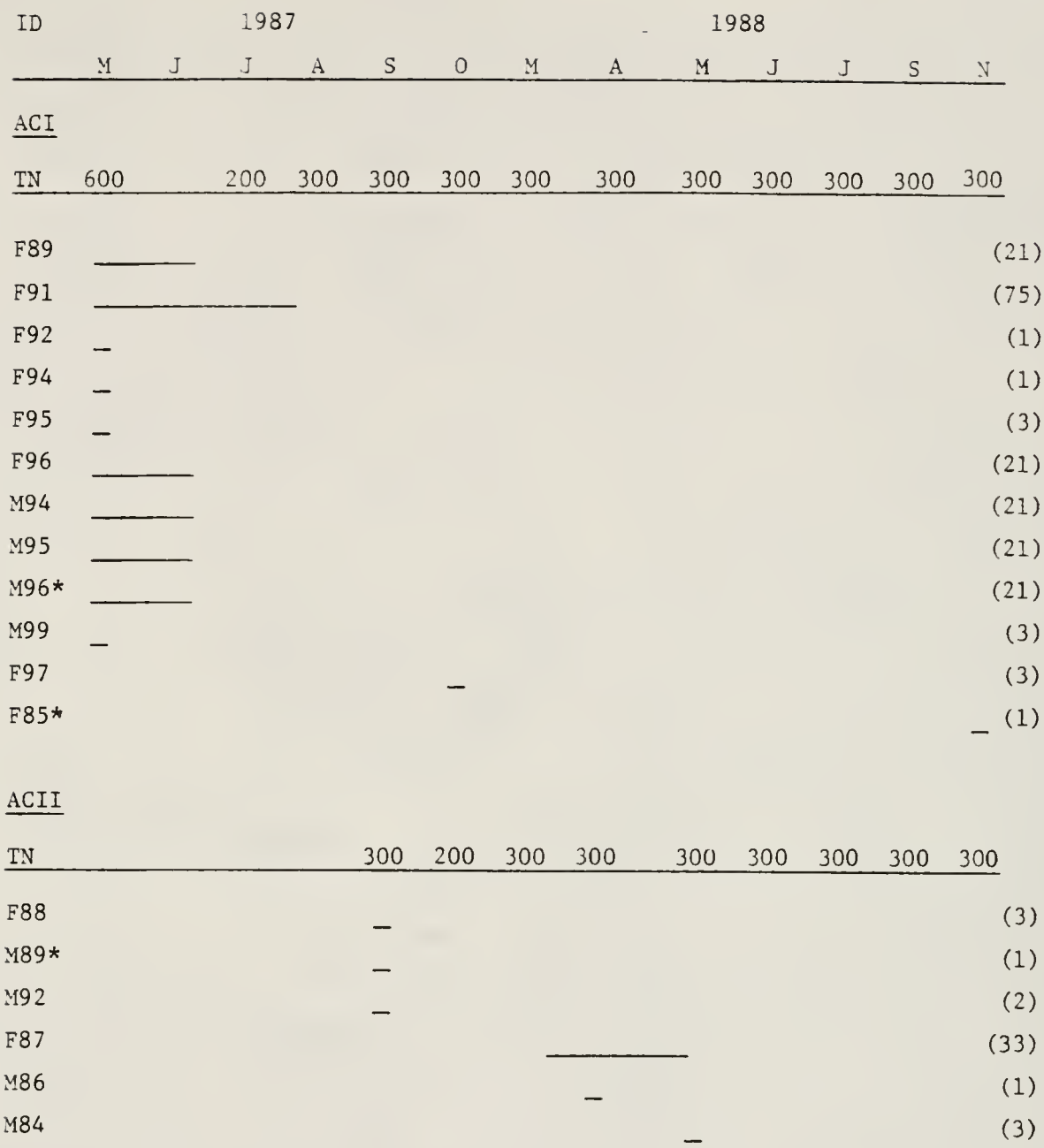


Fig. 7. Trapping data for Podomys on the ACI, ACII, and SL grids. ID indicates sex and identification number; asterisks indicate animals first captured as juveniles; TN indicates trapnights per month; and persistence on grid in days is shown in parentheses.

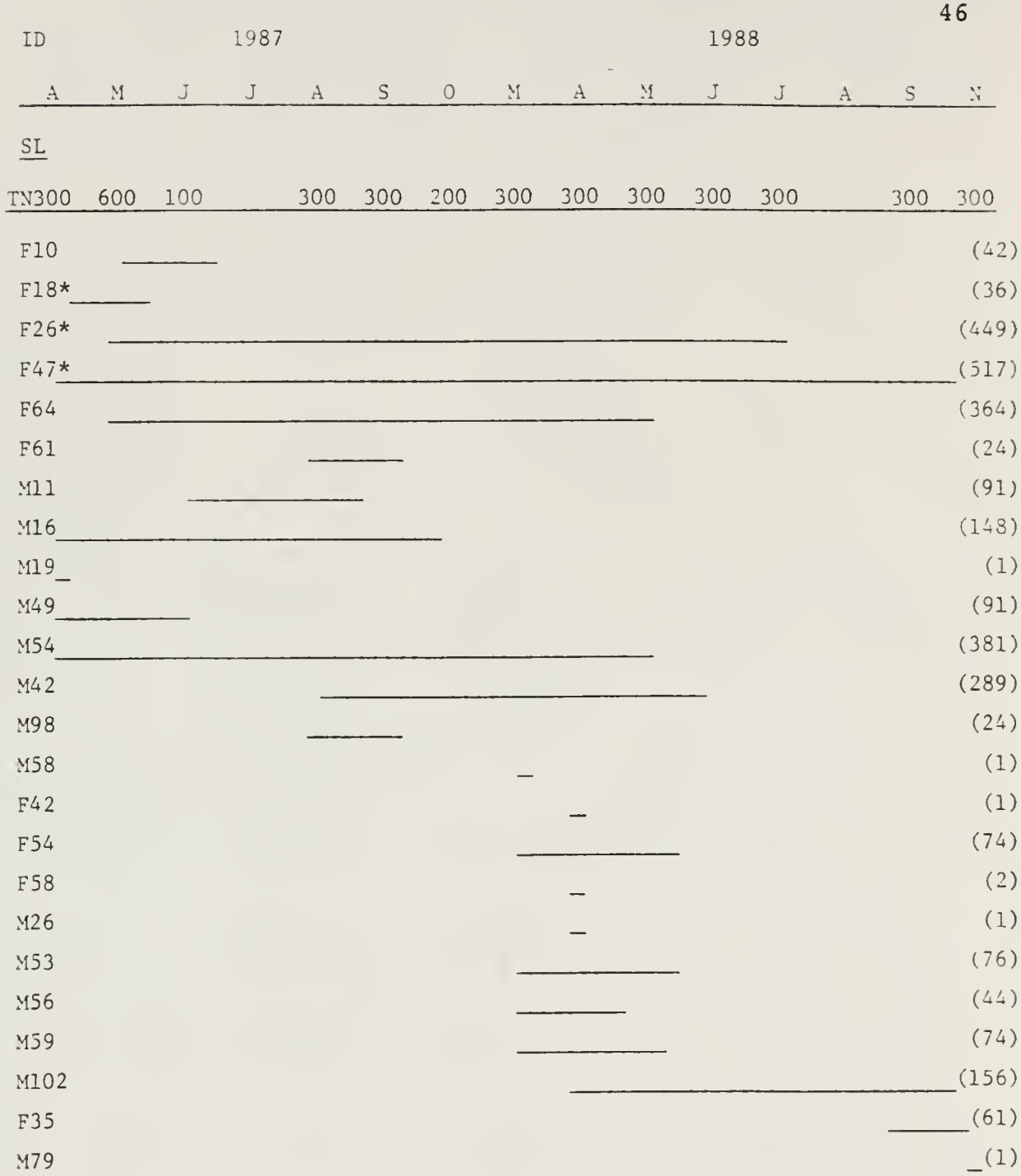


Fig. 7-- continued

strip, and minimum area methods of calculating home range area and she determined that the minimum area method underestimated home range size by 64%, and the exclusive and inclusive boundary methods overestimated home range size by 2%, and 17%, respectively.

On ACII only one individual (female 87 on Fig. 7) was captured at least four times. However, her last two captures occurred across the grid from the first three, and this pattern suggests dispersal rather than a large home range, so I did not include her in the analysis. Home range data are summarized on Tables 5 and 6. Three animals were marked on the grids as juveniles (gray pelage) and died or dispersed off the grid at approximately 60 days of age. Two more animals (female 26 and male 54 at SL) marked as juveniles did not leave the grid. The male shifted his home range, but I could not distinguish between juvenile and adult home ranges for female 26, who subsequently appeared to have an activity area larger than that of other females. Seventeen adults trapped on the two grids (ACI and SL) had an average home range of 804 m^2. In general, males (mean = 910 m^2) appeared to have larger home ranges than females (mean = 683 m^2), but the difference was not significant (Mann-Whitney test at $p = 0.01$).

To determine whether ranges of females and males overlapped, I plotted home ranges of Podomys caught during May 1987 on ACI and May 1987, September 1987, and May 1988 on SL

TABLE 5. Home range data for 20 Podomys trapped on two grids. Id is the identification number, N_G is the number of captures, P_G is the persistence on the grid in days, A is the area of the home range in m^2 for juveniles (A_J) and adults (A_A).

Grid	Id	Sex	N_G	P_G	A_A	A_J
ACI	89	F	6	21	700	
ACI	91	F	7	75	500	
ACI	96	F	4	21	400	
ACI	94	F	6	21	916	
ACI	95	M	5	21	750	
ACI	96	M	5	21		800
SL	61	F	5	24	1000	
SL	10	F	6	42		500
SL	18	F	6	36		600
SL	26	F	17	449	1350	
SL	47	F	12	517	300	
SL	54	F	6	74	300	
SL	42	M	8	289	1850	
SL	49	M	10	91	1200	
SL	54	M	16	381	1093	200
SL	16	M	9	148	800	
SL	53	M	6	76	600	
SL	56	M	7	44	500	
SL	59	M	8	74	1000	
SL	102	M	10	156	400	

TABLE 6. Capture data for 36 Podomys at Anderson-Cue. ID indicates sex and identification number; YR is year of first capture; AGE is age at first capture (juvenile, subadult, or adult); N is number of captures at grids (N_G), burrows (N_B), and total (N_T); P is persistence, in days, on grids (P_G), burrows (P_B), and total (P_T). Asterisks indicate trap mortality.

ID	YR	AGE	N_B	P_B	N_G	P_G	N_T	P_T
F83	88	J	1	1			1	1
F84	88	J	3	3			3	3*
F85	88	J			1	1	1	1
F86	88	A	7	109			7	109
F87	88	SA	2	2	5	33	7	33
F88	87	A	1	1	3	3	4	9
F89	87	A			6	21	6	21
F90	87	SA	1	1			1	1
F91	87	SA			7	75	7	75
F92	87	A			1	1	1	1
F93	87	A	1	1			1	1
F94	87	A	7	164	1	1	8	164
F95	87	A	1	1	3	3	4	21
F96	87	A	1	1	4	21	5	40
F97	87	A	9	171	3	3	12	193
F98	87	J	1	1			1	1
F99	87	A	1	1			1	1
F100	87	SA	4	124			4	124

TABLE 6---continued

ID	YR	AGE	N_B	P_B	N_G	P_G	N_T	P_T
M80	88	SA	3	216			3	216
M84	88	A	2	39	2	3	4	39
M85	88	SA	3	101			3	101
M86	88	SA			1	1	1	1
M87	88	SA	2	2			2	2
M40	87	A	1	1			1	1
M88	87	J	1	1			1	1
M89	87	J			1	1	1	1
M90	87	J	1	1			1	1
M92	87	A	3	48	2	2	5	48
M93	87	SA			3	5	3	5*
M94	87	A	2	106	6	21	8	106
M95	87	A			5	21	5	21
M96	87	J			5	21	5	21
M97	87	A	4	150			4	150
M98	87	?	1	1			1	1
M99	87	SA	1	1	3	3	4	21
M100	87	A	1	1			1	1

(Fig. 8), the three months during which populations appeared to be the largest (Fig. 7). Generally, ranges of males and females overlapped, but ranges of adult females did not (except occasionally with juveniles or young adults), a pattern which suggests intra-sexual territoriality (Kaufmann, 1983). A female juvenile (female 18) overlapped with the ranges of an adult of each sex (Fig. 8A). Female 26, the one with the unusually large range, overlapped somewhat with female 61 in September 1987. The only males that overlapped were three males at SL (Fig. 8C), two of which possibly were siblings.

Trapping at Burrows

With the data from trapping at burrows, I estimated home ranges by mapping movements of adults trapped more than four times in a year on AC and SL, using the exclusive boundary method (Stickel, 1954) as I did for grids. For burrows on the perimeter of the study site, I plotted a boundary of 10 m (which I considered a conservative estimate of distance moved beyond the burrow). All capture points were weighted equally, but in a few instances I omitted points that suggested unusual forays outside the usual home range of the animal. I then measured the home range area with a Lasico Compensating Planimeter.

Seventy-five home ranges for 62 animals who fit the above criteria, including three females on AC, are shown in

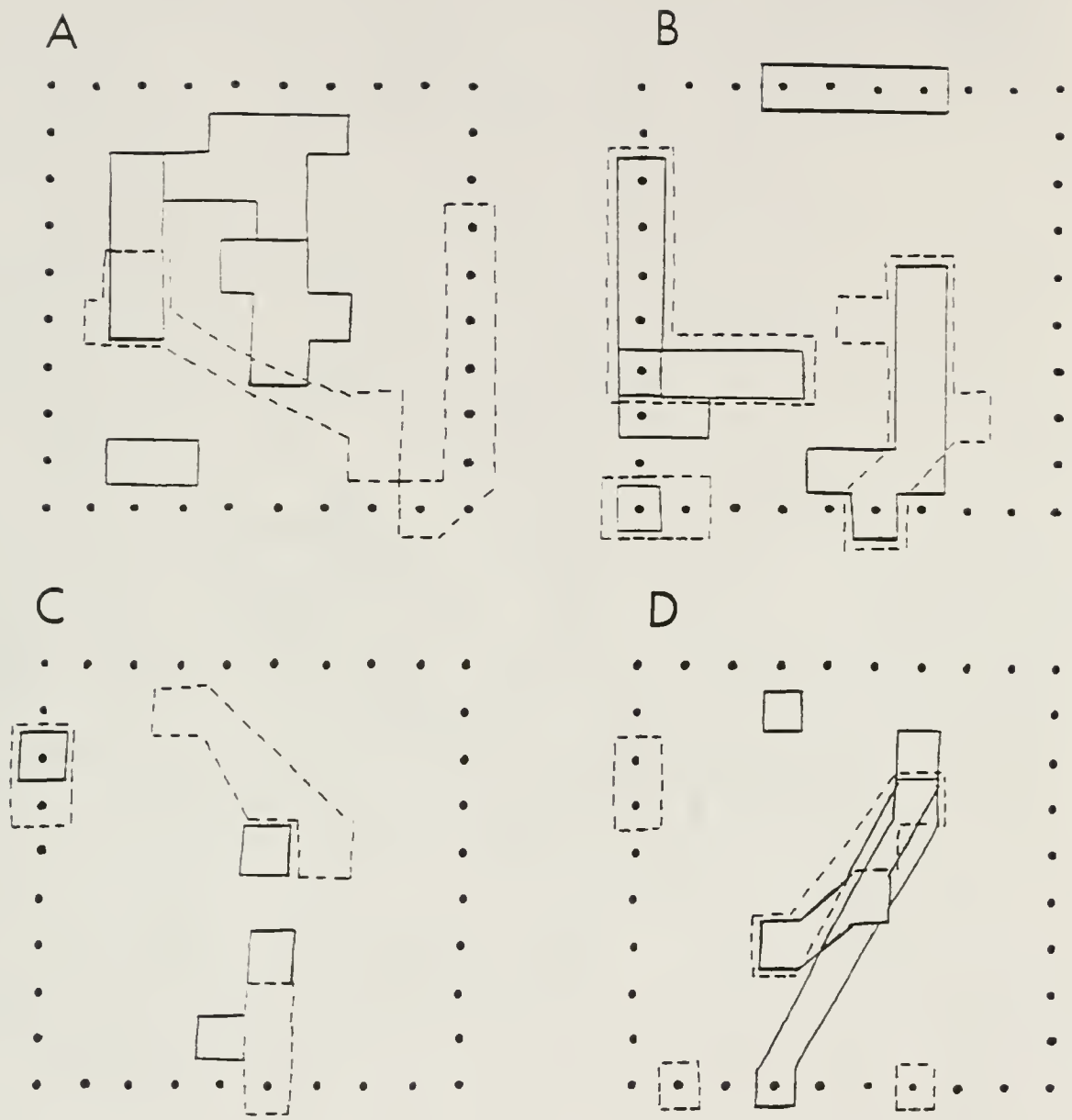


Fig. 8. Home ranges of Podomys trapped on the ACI grid in May 1987 (A) (n = 6 mice, 600 trapnights) and on the SL grid in May 1987 (b) (n = 8, 600 trapnights), May 1988 (c) (n = 9, 300 trapnights), and September 1987 (D) (n = 7, 300 trapnights). Dots represent the outer boundary of grid. Solid lines represent home ranges of females, dotted lines those of males.

Fig. 9. Home ranges for adult males frequently overlapped, but those of females did not; two SL females who appear to overlap in 1988 actually were separated temporally. This separation of home ranges, similar to that observed on grids, suggests intra-sexual territoriality. Animals who survived more than one year (e.g., SL male 11 in 1985-87) showed fidelity to the same general area every year. Home ranges varied in size from 210 m^2 (for SL female 26, captured at a single burrow 6 times in 1987) to 11007 m^2 (for SL male 11 in 1986). The average home range size for 35 females was 2601 m^2 (SD = 1315.1) and for 40 males was 4042 m^2 (SD = 2269.4); home range size of the two sexes differed significantly (Mann-Whitney U = 2.95, p = 0.01). For the SL data I also compared areas in 1983-85 with those of 1986-88 to see whether home range size changed after the prescribed burn in 1985, but I found no significant difference.

Capture data for the 62 mice whose home ranges were mapped are shown on Table 7. Females 86, 94, and 97 (1987) were from AC; the remaining animals were on SL. Each animal was trapped from 5 to 22 times during the year in question, and almost all mice utilized more than one burrow (mean number of burrows = 3.8). Estimates of persistence (P_B) were calculated by counting the number of days between first and last captures spent by the animal in the area shown on the figure. These estimates of persistence are not comparable across years because trapping effort varied each

Fig. 9. Annual home ranges of 62 Podomys on the SL sandhill, 1983-1988. Dots represent tortoise burrows where mice were trapped. Solid lines indicate home ranges of females, dashed line for males; a) 1983, 52 burrows; b) 1984, 61 burrows; c) 1985, 89 burrows; d) 1986, 103 burrows; e) 1987, 131 burrows; f) 1988, 136 burrows. Bar represents 20 m.

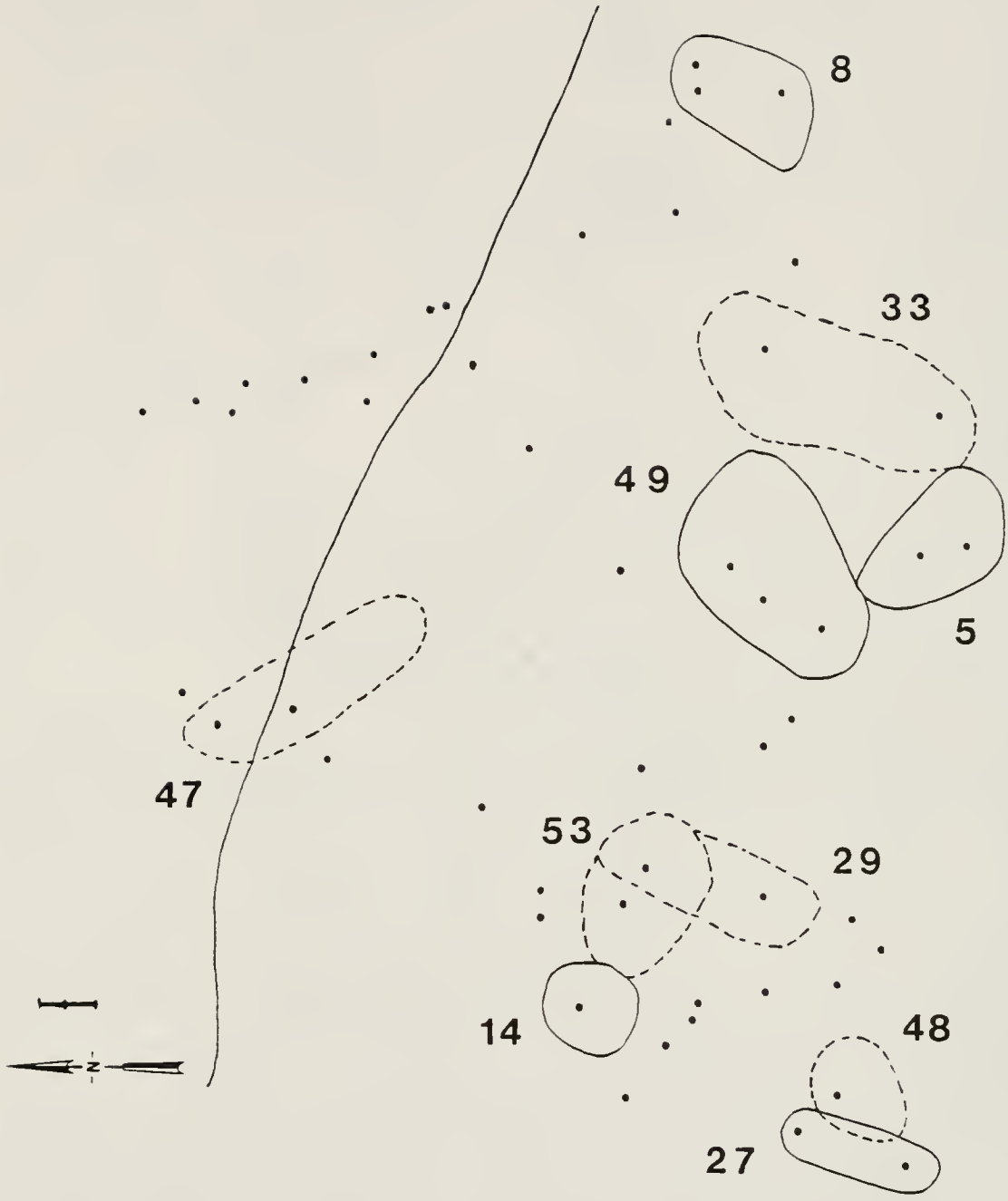


Fig. 9a.

Fig. 9b.

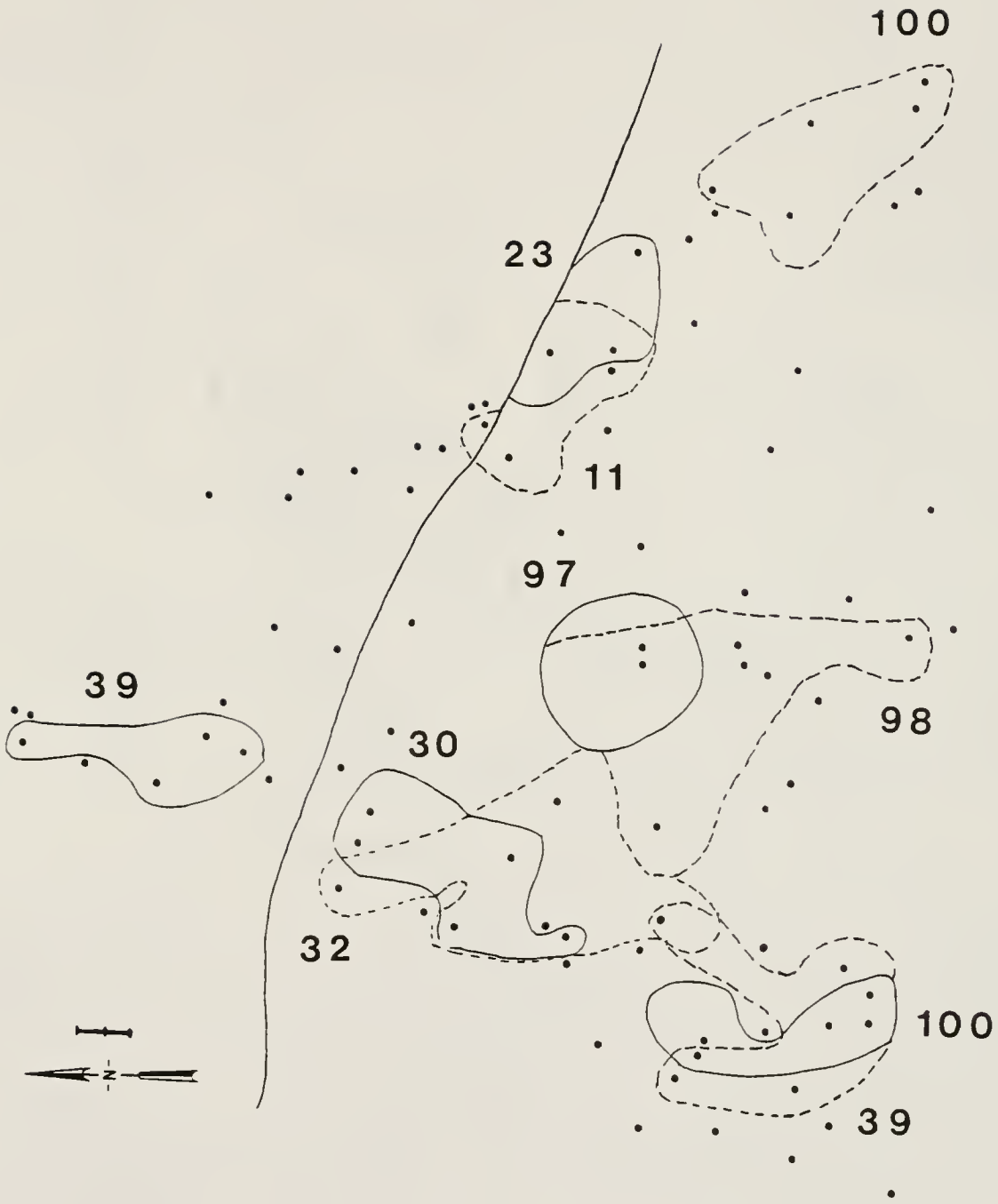


Fig. 9c.

Fig. 9d.

Fig. 9e.

Fig. 9f.

TABLE 7. Capture data for the 62 adults whose home ranges are shown on Fig. 9. ID is the sex and identification number of each mouse; YEAR is the year for which the home range was calculated; N_B is the number of captures, P_B is persistence (in days); $\#_B$ is the number of burrows where each animal was caught; and asterisks denote animals present when trapping ceased in November 1988.

ID	YEAR	N_B	P_B	$\#_B$
F5	1983	5	93	2
F8		6	71	3
F14		6	71	2
F27		5	114	2
F49		5	117	4
M29		5	79	2
M33		5	79	2
M47		5	99	2
M48		5	100	1
M53		5	79	2
F23	1984	8	125	2
F29		11	139	5
F34		5	56	2
F38		5	49	2
F43		15	222	3
M25		6	135	3
M27		5	61	3
M28		5	63	2
M39		14	171	5

TABLE 7--continued

ID	YEAR	N_B	P_B	$\#_B$
M48		12	211	8
M85		6	99	3
F23	1985	14	212	3
F39		12	84	4
F30		8	183	5
F97		8	185	3
F100		22	265	5
M11		16	253	5
M32		13	183	6
M39		18	265	7
M98		13	265	6
M100		7	100	5
F89	1986	5	49	2
F93		5	36	3
F94		8	103	4
F95		6	107	2
M11		19	253	8
M72		5	68	3
M73		7	79	3
M76		11	133	7
M80		12	103	7
M88		16	259	4
M97		5	101	3

TABLE 7--continued

ID	YEAR	N_B	P_B	$\#_B$
M98		5	171	3
F26	1987	6	78	1
F47		8	113	2
F61		7	243	3
F68		6	170	5
F72		5	125	3
F86		7	109	4
F94		7	164	6
F97		9	171	8
M11		8	143	5
M16		7	233	3
M17		5	193	2
M42		5	31	5
M57		9	242	3
M65		7	213	4
M80		9	201	5
M98		5	218	4
F10	1988	11	227*	4
F26		14	193	6
F36		5	94	3
F37		9	121	5
F46		10	151	5
F47		11	193	2

TABLE 7--continued

ID	YEAR	N_B	P_B	$\#_B$
F49		8	148*	3
F52		11	151	5
M20		8	151	4
M22		8	151	7
M25		7	132	4
M34		6	104	4
M37		9	148*	5
M42		11	198*	7
M51		10	151	4
M102		13	198*	2

year; nor do they represent longevity because captures of juveniles and subadults (or captures as adults in years other than those shown) are excluded. The P_B values are useful as minimal estimates of persistence on the sandhill.

Conclusions

Fluorescent powder was not a useful method of determining the home range of Podomys on Ordway. Powder trails did not indicate the complete area traveled by mice even during one night. Although some data regarding substrate use or social interactions were gathered, considerable time and effort were required. The technique proved successful with smaller Peromyscus (Lemen and Freeman, 1985, 1986), so I suspect the failure at Ordway was not related to the body size or biology of Podomys, but possibly to density or structure of vegetation.

Trapping on grids provided estimates of home range size and persistence, as well as demonstrating the exclusivity of home ranges of adult females. There also was evidence that males had larger home ranges that occasionally overlapped with each other and with females. However, estimates of home range areas obtained from trapping at burrows suggest that estimates from grids were too small. Evidently the "standard" mammal-trapping grid (10000 m^2 with 10-m trap intervals) was insufficient to measure home ranges of Podomys in sandhills. Doubling the trap interval to 20 m would

produce a 10 row by 10 column grid covering 40000 m^2, which would encompass mean home ranges estimated at burrows for females (2601 m^2) and males (4042 m^2), might be more useful. No fewer than 100 trap stations should be used. However, one should keep in mind that increasing grid size on some sandhills will spread the grid into neighboring habitats, and that trap success on the grid will be smaller than on the burrows.

Trapping at burrows produced larger estimates of home range size than I expected, but the means are not unreasonably large when compared with other values reported for Peromyscus. Stickel (1968) reported that home ranges of Peromyscus varied from 0.1 to 10 acres. Hoffmeister (1981) reported mean home ranges for female (8290 m^2 +/- 2688) and male (10465 m^2 +/- 4043) P. truei in pinon-juniper habitat, also using the exclusive boundary strip method. Although the range of home areas of Podomys varies considerably, further research might show that my means are underestimates, based as they are on many individuals located on the edges of my study sites. I also have no measure of vertical habitat use; for example; it would be interesting to determine whether the mice occupy a larger home range volume in years when acorns are produced.

In analyses of both burrow and grid data, I omitted animals that were recaptured less than three times. A possible consequence of this approach is that several animals

might occupy the same space. However, the fact that both sets of data show abutment of home ranges of adult females seems good evidence of mutually exclusive home ranges, which suggests that females might be territorial.

DIET

Field Observations

Almost nothing is known about the natural diet of Podomys. Merriam (1890) reported an observation that mice in the southeast ate the seeds of "scrub-palmettoes." Layne (1970) and Humphrey et al. (1985) suggested that acorns might be a major food source during mating years, based on the association of P. floridanus with habitats with Q. laevis and other oaks. Milstrey (1987) reported that captive Podomys ate engorged soft ticks (Ornithodoros turicata americanus) that parasitize gopher frogs and tortoises, raising the possibility that these mice prey on other residents of Gopherus burrows. Other foods presumably include insects, seeds, nuts, fungi, and other plant material (Layne, 1978).

Five field observations at SL provided additional dietary information. An adult male caught and released on the grid (5 May 1988) readily ate a cricket (Gryllinae) I offered to him. On 15 June 1987 at approximately 0245 EST, an adult female (who had been trapped, powdered, and released) caught a small moth and consumed all but the wings. On 9 May, an adult female just released from a trap ate a

young shoot of Smilax auriculatus. On 20 July 1987, at burrow #15, I also observed an adult male take a fruit of the flag pawpaw (Asimina incarna) (Jones, 1989). After being released from the trap, this mouse climbed 30 cm up a plant on the apron of the burrow, and knocked a ripe pawpaw to the ground. He then ran down, picked up the pawpaw, and carried it 11.4 m to burrow #71. In July 1988 another mouse took a pawpaw, again at SL. A female released from a trap at a burrow hid in a hole at the base of a turkey oak approximately 5 m NW of the burrow. In a few minutes she left the hole, picked up a small pawpaw fruit (A. incarna), and carried it back to the hole and nibbled on it.

Predation and dispersal of Asimina fruits have not been well studied. Willson and Schemske (1980) reported opossums and raccoons sampling unripe fruits of A. triloba in Illinois. Norman and Clayton (1986) suggested that small mammals probably help disperse Asimina in Florida and reported an observation of Gopherus eating ripe fruits. Human consumption of A. incarna was reported by Bartram (1791). Whether Podomys disperse these fruits, and whether pawpaws are a significant source of food, remains unknown. Willson and Schemske (1980) measured a caloric content of 4.5 kcal/g for fruits of A. triloba in Illinois; fruits ranged in size from 2.1 to 48 g dry weight. Fruit set for A. obovata, A. pygmaea, and A. triloba is less than 10% (Willson and Schemske, 1980; Norman and Clayton 1986). To the best of my

knowledge, nutritional values and fruit set have not been reported for A. incarna, the most abundant pawpaw on Ordway. However, pawpaws certainly are the largest fruits produced in the high pine; surely they represent a significant addition to the summer diet of Podomys.

Laboratory Observations

The maintenance diet of captive animals consisted of rodent chow (Wayne Rodent Blox) and water provided ad libitem. This diet was supplemented with lettuce, carrots, apples, strawberries, sunflower seeds, mixed bird seed, oatmeal, rice, mealworms, crickets, and acorns (Q. michauxi).

In an attempt to determine what mice might eat under natural conditions, I occasionally offered animals fruits and seeds collected at Ordway. All of these offerings were eaten: acorns (Q. chapmanii, Q. geminata, Q. hemisphaerica, Q. laevis, Q. myrtifolia, and Q. nigra), pine seeds (P. elliottii and P. palustris), blueberries (Vaccinium myrsinites), deerberries (V. stamineum), gallberries (Ilex glabra), blackberries (Rubus argutus), gopher apples (Licania michauxii), pawpaw fruits (A. incarna and A. pygmaea), flowers of Stillingia sylvatica, and seed pods of Crotalaria rotundifolia and Galactia elliotti. Seeds and stems of unidentified grass species were shredded and incorporated

into the cotton nesting material, and probably eaten as well.

Predation on vertebrates appears limited to stressful conditions. Eisenberg (unpubl. data) trapped an adult male on SL in 1983 who detached the posterior part of a juvenile red rat snake (Elaphe guttata) that was caught half way in the trap. The mouse ate about 3.5 cm of the snake to the bone. An adult male caught on AC in October 1987 ate the viscera of a juvenile also caught in the trap. I also lost a litter of three young in captivity on the only occasion that I had a male and two pregnant females in the same aquarium.

In general, feeding behavior follows that described for Peromyscus by Eisenberg (1968), in which the animal crouches and manipulates the food with its forepaws. Larger items such as pawpaws are held against the substrate. Seed pods were opened by grasping the pod vertically, resting one end on the substrate, chewing off one end of the pod, and opening the pod longitudinally along a suture. Larger foods, such as turkey oak acorns, are dragged with the incisors; smaller items are carried in the mouth. Some individuals consistently took favored foods (such as acorns and sunflower seeds) to the corners of the aquarium and covered them with kitty litter; I considered this caching behavior. Food items and remains also commonly are found underneath nests.

This ready acceptance of a wide variety of foods implies that P. floridanus is an opportunistic feeder, like Peromyscus. As King (1968) pointed out, we lack systematic studies of taste discrimination and food preferences. For Podomys we also need basic studies (stomach and fecal analyses) to learn more about the natural diet.

Acorn Preference Tests

I performed preference tests to determine whether acorns of turkey oaks (Q. laevis) are preferred over acorns of other species that are less abundant or produce fewer acorns in the high pine. Such a preference might be a partial explanation for the distribution of Podomys in sandhills at Ordway.

For feeding tests, an individual was placed in an aquarium with clean kitty litter, nesting material, water, and rat chow at least 24 hours before beginning the test. To start a trial the chow was removed and three bowls (each containing five acorns of a single species) were added at about 1900 hours. Each acorn was marked and weighed and I measured its height and width with dial calipers. No effort was made to ascertain that all acorns in a bowl were identical in size. Acorns that had weevil holes were not used, and in a single trial all acorns either had caps or lacked them. Approximately 12 hours later I removed the bowls, acorns, and acorn fragments. I recorded whether acorns were

removed from bowls and whether they were opened and eaten, opened and evidently not eaten, gnawed, or apparently untouched. I controlled for location effects by shifting the relative positions of the three types of acorns in each trial.

Two unexpected difficulties arose. The first was the unpredictability of the acorn supply, which made it impossible for me to run tests with identical species in 1988 and 1989. Additionally, the majority of acorns on the ground already contained weevil larvae or were otherwise spoiled. Secondly, I discovered that some of the acorns I tested were spoiled (by insects or by mold) even though they lacked holes. Possibly this spoilage is the reason that some hulls were opened but the meat not removed. For this reason I simplified analysis of results by examining whether acorns were unopened or opened, regardless of whether any of the meat appeared to have been removed. These data were then ranked (rank 1 to the smallest number opened) and the Friedman test (Conover, 1980) was used to test the hypothesis that species of acorns were opened in equal numbers.

In 1988, I concentrated on determining which acorns were eaten by Podomys. I presented acorns from six species of oaks (Chapman's (Q. chapmanii), live (Q. geminata), turkey (Q. laevis), laurel (Q. hemisphaerica), myrtle (Q. myrtifolia), and water oaks (Q. nigra)) to four captive animals. Five of these species belong to the red-oak group,

which generally contains three or four times more tannin (Briggs and Smith, 1989) than species of the white-oak group (which includes Q. chapmanii). Each mouse was presented with turkey oak acorns in combination with acorns from two other species; two to four trials were run per animal for a total of 12 trials. Although the sample is inadequate for statistical analysis, I noted that the mice opened acorns of all species, and in all but one trial turkey oak acorns were opened in the smallest numbers. I then planned to test animals with a combination of acorns from Chapman's, live, and turkey oaks, the most prevalent Quercus species on the SL sandhill.

In 1989 Chapman's and live oak acorns were not available, so I gathered acorns from Q. laevis and two different trees of Q. hemisphaerica, one from the old pasture near Ross Lake Bridge and the second from a hammock past Anderson-Cue. I expected that Q. laevis, the predominant acorn-producing species on SL, would be preferred. I tested nine animals, two trials each. For analysis I used results of the first trial only; there was no difference in ranks of first and second trials for any of these mice. Results indicated that acorns were not opened in equal numbers (Friedman test, $T = 26.75$, significant at $p = 0.01$). When the Friedman test indicates rejection of the null hypothesis, multiple comparisons may be made to determine which treatment is significantly different from the others

(Conover, 1980). For multiple comparisons at a significance level of $p = 0.01$, acorns from Ross Lake (Q. hemisphaerica) were opened significantly more often; differences between the acorns from the hammock and from Q. laevis were not significant. These results indicate not only that the mice preferred laurel oak acorns over turkey oak acorns, but that mice distinguished acorns from two different individuals of Q. hemisphaerica.

The apparent preference for Q. hemisphaerica was surprising in that its acorns contain more tannic acid than Q. laevis (Harris and Skoog, 1980). The laurel acorns were smaller than the turkey oaks', so possibly the preference is due to differences in handling time. Another possibility is selection according to chemical composition other than tannin content. Halls (1977) reported that Q. laurifolia (= Q. hemisphaerica) had higher fat and carbohydrate content than Q. chapmanii and Q. incana; unfortunately, values for Q. laevis were not listed. Possibly my results were some artifact of using captive animals. However, in the only published study of acorn preference in Peromyscus, Briggs and Smith (1989) found that five P. leucopus captured in habitats lacking oaks consumed equal amounts of acorns from species of the red and white oak groups. Peromyscus caught in areas containing oak trees selected acorns of Quercus species found in their habitat, independent of fat, protein,

and tannin content. These results lead me to believe that there is some real difference between the acorns I used.

Except for smaller acorns that occasionally were split in half, acorns were opened consistently at the hilum (basal scar). Although acorns typically were carried by the point at the distal end, the mice never chewed open the hull there. For small, round acorns a neat incision was made around the scar; on more elongate nuts (Q. geminata and Q. laevis) the hull might be nibbled farther down the sides. Caps, if present, were removed; there was no difference in the numbers of capped and capless Q. laevis acorns opened. Occasionally I found acorns opened in this manner on aprons or near burrow entrances. Hulls of Q. laevis were found in excavated burrows (Jones and Franz, in prep.) and E. Milstrey vacuumed remains of what appear to be Q. geminata and Q. laevis out of burrows on Roberts Ranch, Putnam County; all of these hulls were opened in a manner consistent with what I observed with captive animals. Small piles of emptied hulls occasionally are found at the base of turkey oaks on Ordway; however, it is possible that Glaucomys or birds might make these piles. Of the 450 acorns presented in 30 trials to 13 mice, 66% were removed from bowls, whether opened or not.

I avoided use of acorns that appeared spoiled because mice did not appear to eat blackened nutmeats. I did not test preferences of sound acorns vs. acorns with weevil

larvae. On one occasion an adult female immediately ate a larva from an acorn opened but not eaten by another individual. Semel and Andersen (1988) suggested that such differences in behavior might be due to mice being unable to detect larvae in unopened acorns, or that individuals can detect infestation but some individuals avoid infested nuts. They thought that tooth marks on the hull and movement of acorns might represent assessment.

Based on these results, I suggest that acorns of Q. laevis are eaten but other species are preferred if available. Turkey oaks are an unreliable food supply. Umber (1975) noted acorn production of Q. laevis was low and variable on his study site in Citrus/Hernando counties, and Kantola and Humphrey (in prep.) found that trees on low slopes at Ordway produced significantly more acorns than trees on higher slopes. Layne (in press) correlated the relatively greater abundance of Podomys in scrub and scrubby flatwoods with higher and more consistent acorn production than in the high pine. Proximity to Q. geminata and other acorn-producers might be a partial explanation for the relatively higher and more constant population of Podomys at SL than at AC and BP. If oak species in hammocks are more reliable producers, the restriction of P. gossypinus and Ochrotomys nuttali to hammocks at Ordway might be partly due to the food supply. This leads to the hypothesis that competition, possibly linked with other factors such as

predation, forces Podomys into the high pine when the other rodents are present.

Supplemental Feeding Experiment

Are Podomys limited by food supplies? If food is a limiting factor, mice should respond to extra food with an increase in numbers, increased individual mass, and an extended breeding season. A food limitation could partly explain population sizes and distributions at Ordway. I attempted an experiment of food supplementation using foods favored by captive Podomys. The only supplementation experiment that has been done with the Florida mouse was that by Young (described in Young, 1983 and Young and Stout, 1986) on two grids in sand pine scrub in Orange County. Other rodents responded to the additional food, but Podomys rarely appeared on Young's grids and failed to establish a permanent population during the experiment, although the species had been abundant on both grids before the study (Young, 1983). She concluded that Florida mouse populations were limited by factors other than food.

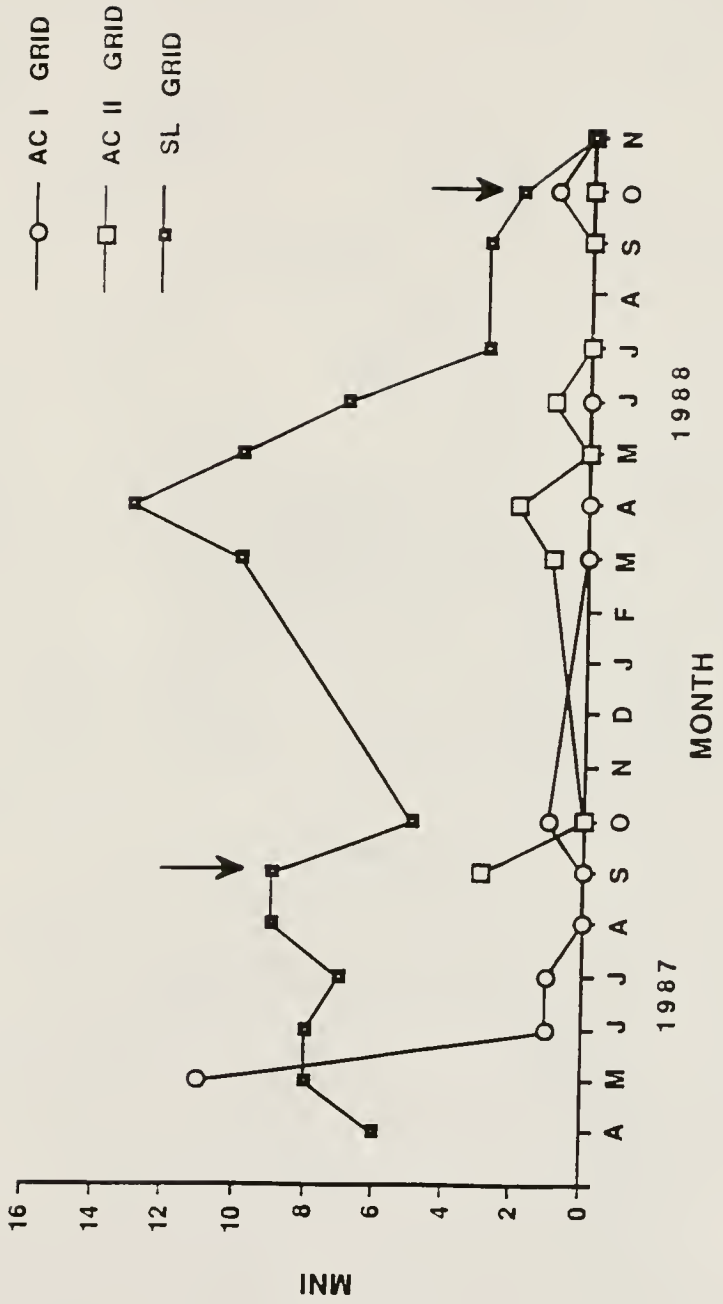
My experimental design consisted of three grids, two on the AC and one on the SL sandhill. Trapping procedure was described under Home Range. The last grid (SLII) was set on the SL sandhill west of Breezeway Pond. Prior trapping at burrows in each of these areas indicated that mice were present. In April, May, and June of 1988 I trapped SLI for

800 trapnights to determine how many nights of trapping were needed to obtain all animals on the site. Consequently, SLI, ACI, and ACII were trapped for three consecutive nights per month for a total of 300 trapnights monthly. On ACI a mixture of sunflower seeds, mixed bird seed, and oatmeal was provided for one year in seven chick feeders fitted with glass jars. To eliminate non-target species, plastic buckets with two one-inch holes cut near the rims were upended over the feeders and weighted down with a cinder block. I checked feeders periodically and refilled as needed.

The results of this experiment are shown in Fig. 10. Capture rates declined sharply on AC and were highly variable on SL. I had intended to provide food on a second grid (SLII, west of Breezeway Pond). However, 208 trapnights on this grid and surrounding burrows in May, July, and August resulted in the capture of one Podomys. The lack of success on ACI led me to abandon SLII although I continued to provide food on ACI until the end of the 1988 trapping year. On the AC sandhill I continued to trap mice in small numbers at burrows west and east of ACI. Clearly, mice were not obtaining the food or some other factor kept them out of the grid area in spite of obtaining food.

Maximum trapping success for a single night was 9%, but success was usually much lower. Additionally, I captured non-target species, including Sceloporus undulatus, Coluber constrictor, and Glaucomys volans. In spite of the low trap

Fig. 10. Minimum numbers of individuals (MNI) on the ACI, ACII, and SL grids. Arrows indicate beginning and ending of food supplementation on ACI.


AC I GRID
AC II GRID
SL GRID
MNI
16
14
12
10
8
6
4
2
0
A M J J A S O N D J F M A M J J A S O N
1987
1988
MONTH

success I attempted to estimate the persistence (i.e., the time between first and last captures) of mice on the three grids (Table 8). Because these were not closed grids, disappearance of an animal might be due to death, dispersal, or to not entering traps.

TABLE 8. Persistence data for animals on grids. Data presented are minimum number known alive (MNA), mean +/- SD days spent on a grid (maximum values in parentheses), and total numbers of trapnights (TN).

Grid	MNA	PERSIST	TN
ACI	12	16.00 +/- 20.86 (75)	4200
ACII	6	7.17 +/- 12.68 (33)	3000
SLI	24	122.75 +/- 155.7 (517)	4100

ANALYSES OF VEGETATION

Sampling Technique

Can the local distribution of Podomys be predicted on the basis of vegetation structure or species composition? Vegetation was sampled in circular quadrats (radius = 10 m, area = 314.159 m^2) set with tortoise burrows as center points. In the absence of large numbers of trees, circular quadrats are laid out easily using a center pole at the burrow and a rotating radius line; forestry flags were used to delineate the quadrat. Quadrat size was based on preliminary estimates of activity areas obtained by dusting Podomys with fluorescent powder. Although one animal ranged at least 28 m from his burrow in one night (see Home Range above), I decided a radius of 10 m was sufficient to contain significant numbers of plants and small enough to allow me to feasibly obtain counts and identifications of plant species. When I began these samples in 1985 I was uncertain that burrows were distributed randomly, so point-quarter sampling seemed inappropriate. Without knowing the shape of Podomys activity areas, I felt that line-intercept sampling and belt transects would be less representative of areas encountered by mice than circular quadrats.

Sandhills on the Ordway Preserve have been subjected to logging, grazing, suppression of fire, and prescribed burning on different rotations. Cessation of fire, or the frequency of prescribed burns and other activities, affect plant species composition and density on sandhills (e.g., Myers, 1985; Gates and Tanner, 1988). To determine how burrow use changes with successional changes in vegetation, I examined quadrats at SL in 1985, 1987, and 1988. SL has been burned and the pines bear turpentine scars. Trapping effort was equal among these burrows within each year but not among years. Initially 29 quadrats were examined; this number was reduced to 27 after a large oak fell over one burrow and a clearcut was performed at a burrow under a powerline. To see how Podomys behaved at burrows on a sandhill where logging occurred, I set quadrats at 15 burrows at BP in 1988.

I selected burrows so as to include burrows of all three classes of tortoise activity (active, inactive, or old, as defined by Auffenberg and Franz, 1982). Within each quadrat, I counted stems of all woody species (Table 9) in three size categories (tree = dbh > 7.6 cm, sapling = height > 1 m and dbh < 7.6 cm, and seedlings = height < 1 m). I noted the presence or absence of woody debris, including fallen branches or trees, or rotting logs. I estimated the per cent ground cover of bare ground, wiregrass, and gopher apple using five categories (I = 0-10%, II = 10-25%,

TABLE 9. Habitat variables measured in each quadrat. Prime signs indicate variables used in discriminant analyses.

Variable (abbreviation)	Description
Location (LOC)'	BP or SL sandhill
Year (YR)'	1985, 1987, or 1988
Burrow (BUR)'	Identification number
Orientation (ORI)'	Compass reading away from entrance
Sand pine (SP)'	Total stem count (*P. clausa*)
Slash pine (HP)	" (*P. elliotti*)
Longleaf pine (LP)'	" (*P. palustris*)
Loblolly pine (YP)	" (*P. taeda*)
Bluejack oaks (BO)'	" (*Q. incana*)
Turkey oaks (TO)'	" (*Q. laevis*)
Laurel oaks (LA)	" (*Q. laurifolia*)
Post oaks (PO)	" (*Q. stellata*)
Live oaks (LO)'	" (*Q. geminata*)
Persimmon (PER)'	" (*D. virginiana*)
Pawpaws (PAW)'	" (*Asimina* spp.)
Rosemary (RO)'	" (*C. ericoides*)
Sumac (SUM)'	" (*R. copallina*)
Blueberry (VAC)'	" (*V. myrsinites*)
Debris (DEB)'	Presence or absence of fallen logs or branches in each quarter of quadrat (4 indicates presence in all 4 quarters)

TABLE 9--continued

Variable (abbreviation)	Description
Bare ground (GRO)'	Average of categorical estimates of % of bare ground coverage in each quarter of quadrat
Bare ground (ΣGRO)'	Summation of categorical estimates of bare ground coverage per quadrat
Wiregrass (WIR)'	Average of categorical estimates of % of coverage by wiregrass of each quarter of quadrat
Wiregrass (ΣWIR)'	Summation of categorical estimates of wiregrass coverage per quadrat
Gopher apple (GA)'	Average of categorical estimates of % coverage by *Licania* of each quarter of quadrat
Gopher apple (ΣGA)'	Summation of categorical estimates of *Licania* cover per quadrat
Legumes (LEG)'	Total number of species of Fabaceae
Herbs (HERB)'	Total number of all non-woody species

III = 25-50%, IV = 50-75%, V = 75-100%). I grouped species of grasses into five categories (I = Andropogon spp.; II = Panicum hemitonum, III = Panicum (Dicanthelium) spp., IV = Paspalum setaceum, V = Gymnopogon spp.) and sedges into two ("small", such as Bulbostylis warei, and "large", such as Cyperus retrorsus), but did not identify each species. I identified and counted the number of herbaceous species (excluding grasses and sedges), but I did not count stems. All plant species (Appendix) were identified using the plant list compiled for the preserve by David W. Hall and Richard Franz.

I plotted a species-area curve (cumulative number of species vs. cumulative number of samples) for the 1985 data from SL; the curve levelled off after the fifteenth sample, and I concluded that the number and size of quadrats were adequate. I believe smaller sample areas would be inappropriate for two reasons: Hansen (1964) noted that only 8 of 24 burrows he examined had turkey oaks and pines within a radius of approximately 305 cm around the burrow entrance, so larger areas are required to represent trees in the vicinity. Secondly, some quadrats I examined were located at burrows with large aprons, which are disturbed areas that might be favored by certain animals such as Tantilla relicta, Eumeces egregius, and Neoseps reynoldsi (Campbell and Christman, 1982); it is unknown whether these species affect plant distribution on the apron. I suspect that burrow

construction also has some impact on density or heterogeneity of local plant species (perhaps similar to that described at badger excavations by Platt in 1975), although such an effect has not been documented in the literature for Gopherus. Certainly the abundance of some high pine species (such as Eupatorium compositifolium, according to Grelen, 1962 and Hebb, 1971) is affected by other disturbances such as chopping or burning.

Results and Discussion

How did vegetation on the SL plots change between 1985 and 1988? On the burned plots, I expected increased stem counts of woody species and increased numbers of herbaceous species after the 1985 burn. On the unburned plots, I expected little or no change in species composition or density over the three-year period. Frequencies and densities of woody species are shown in Table 10. Two changes were quite evident. Following the fires, particularly the first burn in 1985, numbers of stems of Quercus and Asimina increased. Secondly, mortality of longleaf pine seedlings (P. palustris) obviously was quite high in some areas on both burned and unburned sites due to pine rust in 1986. Stem counts of P. palustris were much lower in 1987 and stem counts of other woody species, such as sumac, increased in the affected areas.

TABLE 10. Frequency (% = percent of quadrats in which a species occurred) and density (# = average number of stems per 314 m^2 quadrat) of woody species identified at SL.

	YEAR Burned plots (n = 22)					
	1985		1987		1988	
	%	#	%	#	%	#
P. clausa	31.8	0.6	18.2	0.2	27.3	0.6
P. palustris	100.0	151.6	100.0	66.9	100.0	81.4
Q. geminata	95.5	66.5	95.5	157.5	95.5	173.8
Q. incana	100.0	88.4	100.0	163.2	100.0	159.9
Q. laevis	100.0	97.8	100.0	174.6	100.0	156.3
Q. laurifolia	13.6	1.5	13.6	3.1	13.6	8.2
Asimina spp.	100.0	40.6	100.0	44.6	100.0	48.7
Ceratiola	31.8	0.9	18.2	0.6	27.3	0.6
Rhus	90.9	86.9	100.0	104.2	95.5	82.9
Diospyros	95.5	34.2	100.0	37.1	100.0	44.8

	YEAR Unburned plots (n = 5)					
	1985		1987		1988	
	%	#	%	#	%	#
P. clausa	0	0	0	0	0	0
P. palustris	100.0	189.4	100.0	141.8	100.0	117.6
Q. geminata	100.0	20.0	100.0	28.4	100.0	28.4
Q. incana	100.0	33.8	100.0	36.4	100.0	43.6
Q. laevis	100.0	153.0	100.0	204.6	100.0	219.8
Q. laurifolia	0	0	0	0	0	0
Asimina spp.	100.0	14.0	100.0	25.4	100.0	25.4
Ceratiola	20.0	0.8	20.0	0.8	20.0	0.8
Rhus	40.0	20.4	40.0	41.2	40.0	28.0
Diospyros	100.0	10.0	100.0	27.4	100.0	31.2

How did vegetation on the BP and SL quadrats differ? SL has more species considered "characteristic" of the high pine environment; the less characteristic species, such as Quercus laurifolia, Q. myrtifolia, Prunus serotina, and Erythrina herbaceae, were found on quadrats at the periphery of the sandhill. The perception that there are fewer longleafs at BP is valid (Table 11). Also, P. clausa and Ceratiola are absent from the BP quadrats, reflecting the low numbers of these species on the BP sandhill. Specimens of P. elliotti and P. taeda, both absent on SL, grow at burrows located on the periphery of the unburned BP site and old pasture. Numbers of turkey oak stems are much greater than on SL and Q. stellata is present. Densities of persimmon (Diospyros virginiana) are somewhat lower on BP; however, the unburned BP quadrats were the only ones containing sapling-sized persimmons. Laessle (1942) and Grelen (1962) noted that Diospyros become more abundant when fires are suppressed and reach greater heights (> 2 m) following disturbance (e.g., chopping) than persimmons on undisturbed sites. The saplings at BP probably reflect a history of fire suppression following logging or some other major disturbance. On BP I observed a few forbs (e.g., Chamaesyce cordifolia, Conyza canadensis, and Rudbeckia hirta) that are associated with disturbed sites, according to Wunderlin (1982); these species were absent or less abundant on SL. However, when I compared the mean numbers of legume species

TABLE 11. Frequency (% = percent of quadrats in which a species occurred) and density (# = average number of stems per 314 m^2 quadrat) of woody plant species identified at BP in 1988.

	Burned plots (n = 9)		Unburned plots (n = 6)	
	%	#	%	#
P. elliotti	0	0	16.7	0.3
P. palustris	11.1	0.2	50.0	2.0
P. taeda	0	0	16.7	0.2
Q. geminata	66.7	37.1	83.3	56.3
Q. incana	66.7	8.7	83.3	20.0
Q. laevis	100.0	521.7	100.0	257.2
Q. laurifolia	0	0	16.7	0.5
Q. stellata	55.6	18.3	33.3	9.3
Asimina spp.	100.0	47.4	100.0	19.0
Rhus	44.4	8.9	66.7	20.7
Diospyros	88.9	33.8	100.0	27.8

and herbaceous species on burned quadrats at BP and SL (1988 samples), I found no significant differences; nor did the unburned quadrats differ significantly in these two parameters. Stem counts of woody species on burned and unburned plots on BP were significantly different (X^2 = 461.03, highly significant at p = .005).

Can numbers of Podomys at particular burrows be predicted based on local vegetation? A univariate analysis was performed to test whether the minimum number of individual mice (MNI) or total number of captures (ALL) could be predicted using variables listed in Table 9. Then a second run was performed using only the 21 parameters shown on Table 12. Because MNI and ALL generally were small, these variables were set to 1 or 2 (if ALL <= 5, then ALL = 1, and if ALL > 5 then ALL = 2; if MNI = 0, then MNI = 1 and if MNI > 0, then MNI = 2). The null hypothesis was that there was no difference between burrows used by mice (MNI > 0) and available habitat, i.e., burrows not used by mice (MNI = 0).

The parameters I used were somewhat useful predictors of ALL (Table 12), but did not predict MNI as accurately. Only four variables (TO, LL, PER, and HERB) had significant ability ($p < 0.05$) to predict ALL. Results of discriminant functions analyses also indicated that these four variables were the most significant. Captures were negatively correlated with stem counts of turkey oaks and longleaf pines, and positively correlated with stem counts of persimmon and

Table 12. Habitat profile of Podomys at all BP and SL burrows where vegetation was sampled. Abbreviations are given in Table 9. Univariate F values are given for analyses between habitat variables and ALL or MNI. N = sample size. *p < 0.05, **p < 0.01, ns not significant.

VAR	ALL	MNI
N	89	89
LOC	0.46	0.02
YR	0.12	4.08*
BUR	0.19	0.15
ORI	0.74	0.15
TO	4.62*	0.41
BO	0.70	0.81
LO	3.45	0.13
LL	4.13*	0.90
PER	10.20**	0.02
SUM	0.47	1.73
PAW	0.83	1.10
DEB	0.18	0.87
ΣGRO	0.48	0.53
GRO	0.71	2.36
ΣWIR	0.30	4.82*
WIR	0.06	4.31*
ΣGA	1.31	1.41
GA	0.12	5.57*
VAC	1.78	0.62
LEG	1.01	0.25
HERB	5.30*	0.83
Wilks' Lambda	0.58	0.70
X^2	41.12	26.91
P	**	ns

numbers of herbaceous species. Stem counts and herbaceous diversity are affected by fire regime; the negative correlation with oaks and pines is consistent with the association of tortoise burrows with open canopy. Most of the other oaks and all the persimmons (except some on unburned quadrats at BP, where ALL = 0) were too small to produce fruits. With the discriminant functions analysis, I classified burrows to the two categories of total number of captures (ALL) (Table 13). With these vegetation variables, 92% of the burrows in ALL <= 5 and 83% of the burrows in ALL > 5 were classified correctly. Using MNI instead of ALL, only 77% of the samples in MNI = 0 and 71% of the samples in MNI > 0 were classified correctly. I repeated the discriminant function analysis using 9 parameters (TO, LO, LL, PER, GRO, WIR, GA, LEG, HERB) representing stem counts of woody species with F > 3.0, ground cover characteristics, and numbers of herbaceous species. With this group of variables, 70% of the burrows in ALL <= 5 and 66% of the burrows in ALL > 5 were classified correctly. Therefore it seems these variables are more useful for predicting relative abundances of Podomys, than for predicting the presence or absence of mice.

I thought it surprising that Podomys did not show a closer correlation with indices reflecting ground cover. I also ran a stepwise multiple regression, using the R^2 criterion to determine the best-fitting regression equation for

TABLE 13. Number (%) of vegetation samples reassigned according to discriminant function analysis to two categories of total number of captures (ALL) of Podomys.

TO:	ALL <= 5	ALL > 5
FROM:		
ALL <= 5	65(92%)	6(8%)
ALL > 5	3(17%)	15(83%)

the two categories of ALL and the independent variables. For the BP samples, the best equation (R^2 = 0.97) was obtained using TO, BO, LO, PER, SUM, PAW, DEB, ΣGRO, ΣWIR, ΣGA, LEG, and HERB. These results must be interpreted cautiously (N = 15, df = 2). For the SL samples, the best equation is obtained if LP also is included (R^2 = 0.85, 0.49, and 0.34 for 1985, 1987, and 1988 samples respectively).

Although BP and SL are both "high pine" or "turkey oak-longleaf pine sandhills", the vegetation on the two sites was not the same. If I had measured abundances of wiregrass and other non-woody species the difference would be more striking. Laessle noted for sandhills (1942:8), "Among the most striking vegetational characters . . . are the small but distinct floristic differences which they show when compared to corresponding communities of the western side of the ridge in central Florida." Of all the Ordway sandhills on which I have found Florida mice (Anderson-Cue, Blue Pond, Longleaf Pine, Rowan, and Smith Lake), no two appear alike in spite of their similar classification. More long-term studies that examine plant-animal interactions are needed to compare the ecology of Podomys on different sandhills.

The burned part of BP appears to be developing into an oak savanna dominated by Q. laevis; given the small number of adult longleafs and the absence of a seed source, it is

unlikely that burning will create a longleaf pine savanna, unless pines are planted (Platt et al., 1988; Rebertus et al., 1989). At SL there appear to be plenty of longleaf pines in all age classes, so possibly adherence to the three-year fire regime will eventually eliminate turkey oaks. However, it is unclear what effect this management policy will have on Podomys. Individuals seemed to persist longer on burned sites, and there was a correlation with stem counts of both oaks (mostly seedlings and saplings) and pines. If oaks represent an important food source, Podomys might persist on a longleaf pine savanna only in low numbers. Additionally, I would expect the decreased abundance and diversity of herbaceous species after the suppression of fire (Hilmon and Hughes, 1965; Gates and Tanner, 1988) to have a negative effect on mouse populations, although we still know little about the Podomys diet.

Tortoises themselves apparently respond to a combination of physical and herbaceous features, in that they prefer abundant ground cover, high herbaceous diversity, sparse shrub cover, and an open canopy, rather than specific plant associations (e.g., Umber 1975; Auffenberg and Franz, 1982; Cox, Inkley, and Kautz, 1987; Breininger et al., 1988). Effects of Gopherus on local vegetation are not well known. Major components of the tortoise diet include Poaceae, Asteraceae, Fabaceae, Pinaceae, and Fagaceae (Garner and Landers 1981; Macdonald and Mushinsky 1988).

Possibly tortoises disperse some food species; Laessle (1944) noted abundant gopher apple seeds around burrow entrances. As mentioned previously, the physical impact of the burrow excavation on the local vegetation has not been studied, although Kalisz and Stone (1984) noted that excavations by burrowing animals help mix nutrients in the soil.

PRESCRIBED BURNS

Materials and Methods

The high pine sandhills of Florida are pyrogenic communities that were subjected to frequent, cool fires. However, aside from the work by Mushinsky (1985) and Gates and Tanner (1988), little is known about the effects of these fires on members of the sandhill fauna besides the gopher tortoise. Taylor (1981) summarized literature regarding effects of prescribed fires on small mammals in the southeast. Although the Florida mouse is listed as a threatened species (Layne, 1978), in only one study (Arata, 1959) were the effects of fire on Podomys examined. Using traplines, Arata trapped for 150 trapnights before the burn and for 1800 trapnights beginning within two weeks after the burn. His trapping success for Podomys was 3% and 9%, before and after the fire respectively.

In my study of habitat preferences by Podomys, I had the opportunity to experimentally determine the effects of fire on Podomys by trapping three sandhills (BP, LP, and SL) before and after prescribed burns. All three sites are on a three-year rotation of prescribed burns; BP is burned in the spring and LP and SL are burned in the late summer. Each of

these sandhills included a small area not to be burned. BP was last burned in 1985. In 1988 we planned to burn BP in May, so I trapped for two months before and after the scheduled date of the burn, at 26 burrows to be burned and 13 burrows in the unburned area across the road. On 24 May there was a lightning strike north of the pond and the Ordway staff spread fire to the rest of the sandhill; the site continued to burn through 25 May. From 27 May through November 1988, I trapped all the BP burrows for a total of 2442 trapnights.

I briefly worked on LP in 1987. I trapped at 18 burrows on the area not to be burned for 375 trapnights between 26 July and 1 November. I trapped at 24 burrows on the side to be burned for 492 trapnights (318 trapnights before the fire on 19 September 1987, and 174 trapnights afterwards). SL was last burned in September 1982; we burned this sandhill again on 10 September 1985. In 1985 I monitored 57 burrows on the area to be burned and 22 burrows on the area not to be burned. During the year of the burn, I trapped on SL for 3092 trapnights, including 2308 on the burned and 784 at the unburned burrows. Because I found trapping success higher at burrows than on transect lines, I continued to trap at burrows. However, comparisons among BP, LP, and SL must be made cautiously. Not only did the number of burrows (hence, trapping effort) vary, but the sandhills differed in

area and seasonality of burns, and the unburned areas were smaller than the burned.

To analyze trapping data, I followed Buech et al. (1977) in calculation of a capture index (CI), which equilibrates trapping effort to 1000 trapnights. They defined CI = number of individuals captured/1000 trap station nights, where a trap station night consisted of two traps at a station for 24 hours. For example, on the SL burn site:

$$\frac{1000 \text{ trapnights}}{805 \text{ trapnights}} \times 19 \text{ animals} = 23.56 = CI$$

I also calculated minimum numbers of individuals (MNI) per 100 trapnights per hectare in an attempt to equilibrate trapping effort and area. The G-test was used to test the null hypothesis that equal numbers of mice were captured on burned and unburned sites.

Description of Procedure for Prescribed Burns

Prescribed burning is a tool used by land managers to sustain a particular type of forest or savanna. Frequently the ultimate goal is to maintain populations of special interest: game and forestry species or threatened and endangered species. For example, in 1982 the Forest Service burned approximately 81000 ha in the Southeast Region alone to enhance habitats used by the red-cockaded woodpecker (U.S. Dep. Agric., 1984). Given these goals, it is not unexpected that the majority of studies that examine how

animals are affected by fire have concentrated on one species of interest, such as quail or white-tailed deer, rather than examining effects on less conspicuous species or on the fauna as a whole.

Humphrey et al. (1985) summarized the management history of the Ordway Preserve. Some sandhills on the property, intended for use as unburned "controls", have been left unburned since at least 1980 when the University of Florida acquired the preserve. The remaining sandhills were placed on a three-year regime of prescribed burns at various seasons. The management goal is to return these sandhills to longleaf pine savannas, as they are believed to have existed (according to Bartram, 1791) before the initiation of logging, farming, and ranching in the area.

On the Ordway, we conducted prescribed burns using drip torches. Fire lines are dropped along roads and fire lanes, and fires burn into the wind. We raked debris away from snags and longleaf pines scarred by turpentine operations. This method produces a relatively cool fire.

Results and Discussion

Apparent densities of Podomys fluctuated monthly on all three sandhills (Figs. 11-13). Numbers of mice were more constant at burned sites than unburned sites. Apparent densities at SL frequently were larger at the unburned burrows; possibly this was a result of the disparity in size of the

Fig. 11. Apparent densities (expressed as minimum numbers of individuals/ha) of Podomys on the burned and unburned areas of the Blue Pond sandhill.

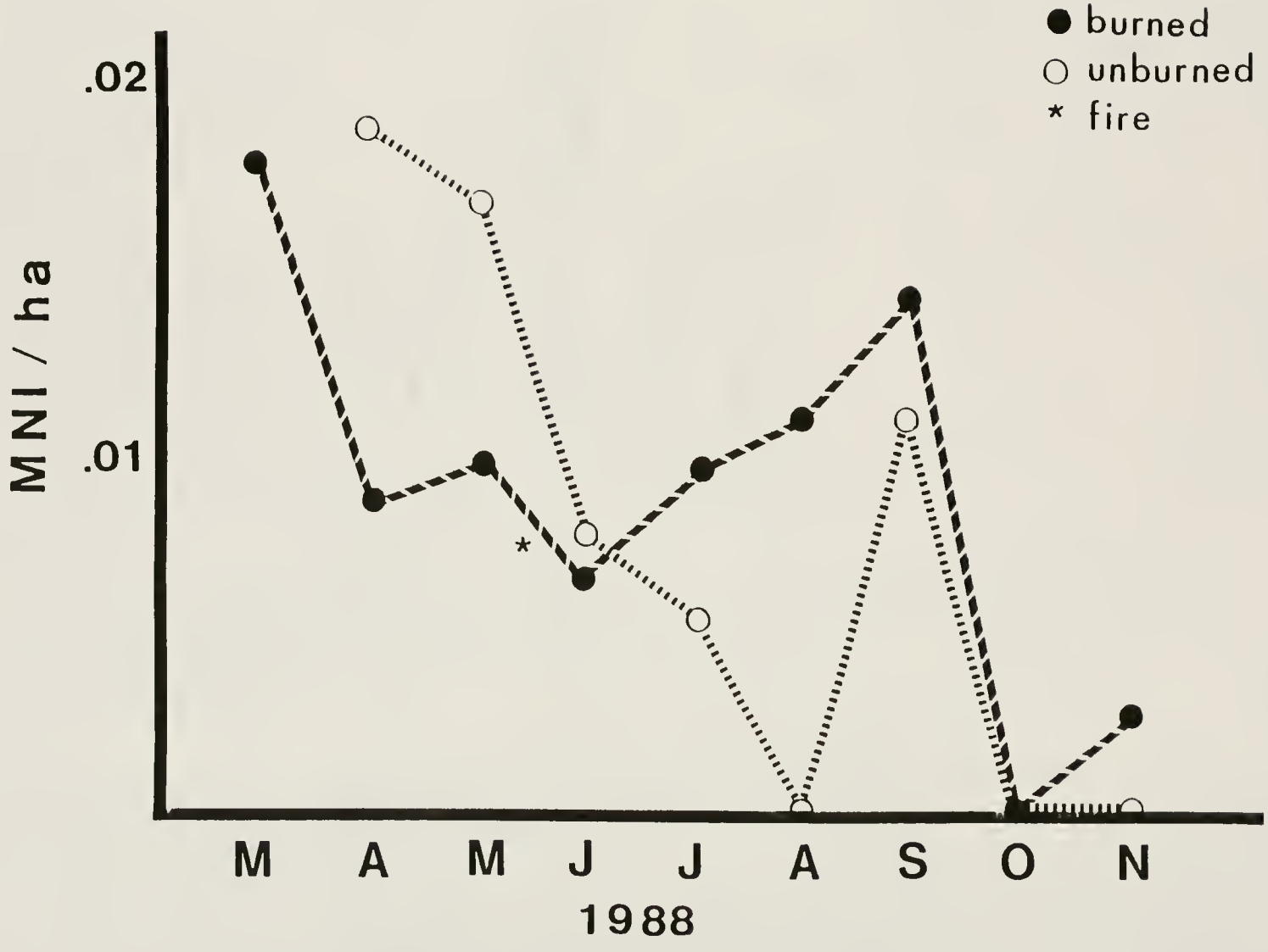

burned
unburned
* fire
.02
.01
MNI / ha
M
A
M
J
J
A
S
O
N
1988

Fig. 12. Apparent densities (expressed as minimum numbers of individuals/ha) of Podomys on the burned and unburned areas of the Longleaf Pine sandhill.

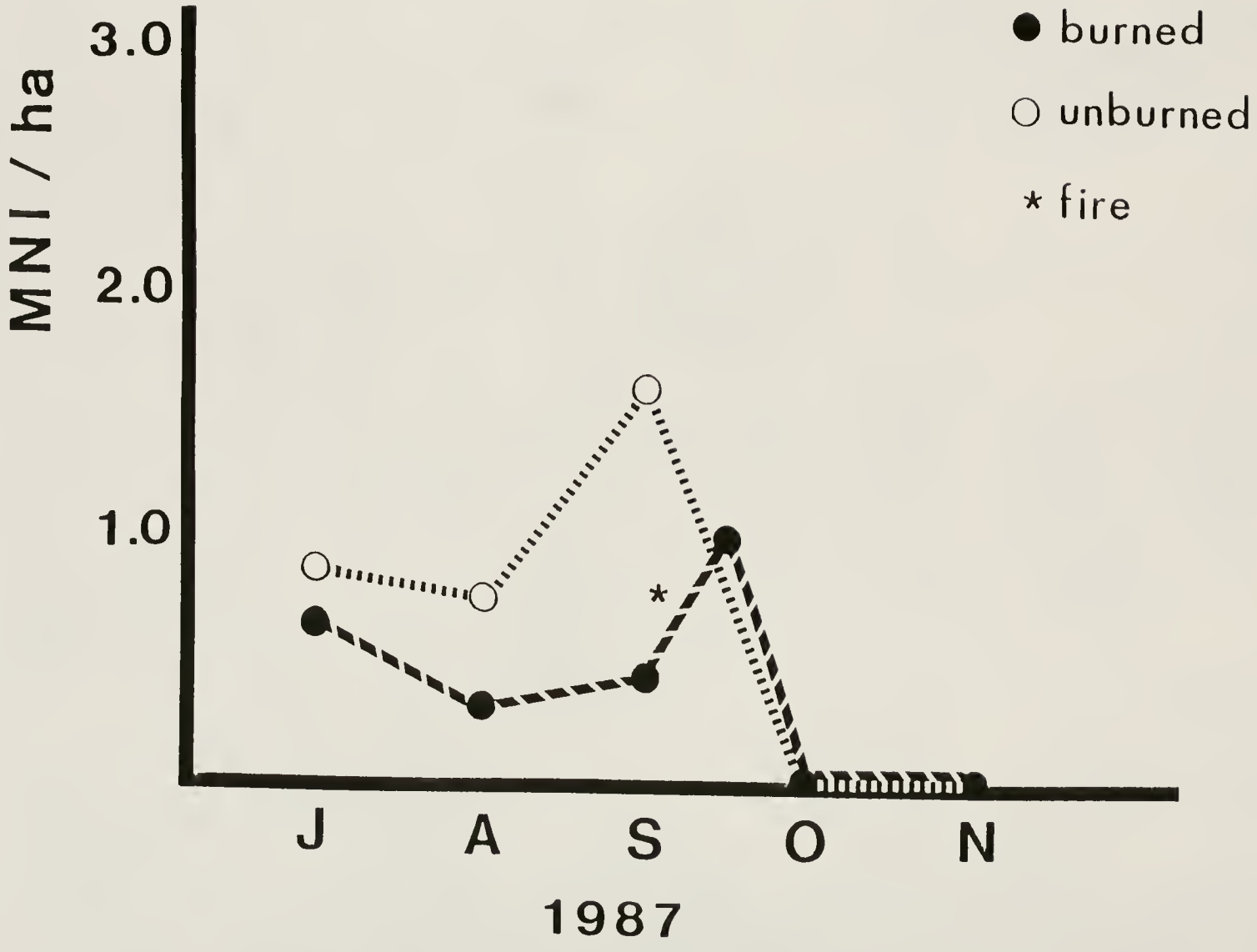
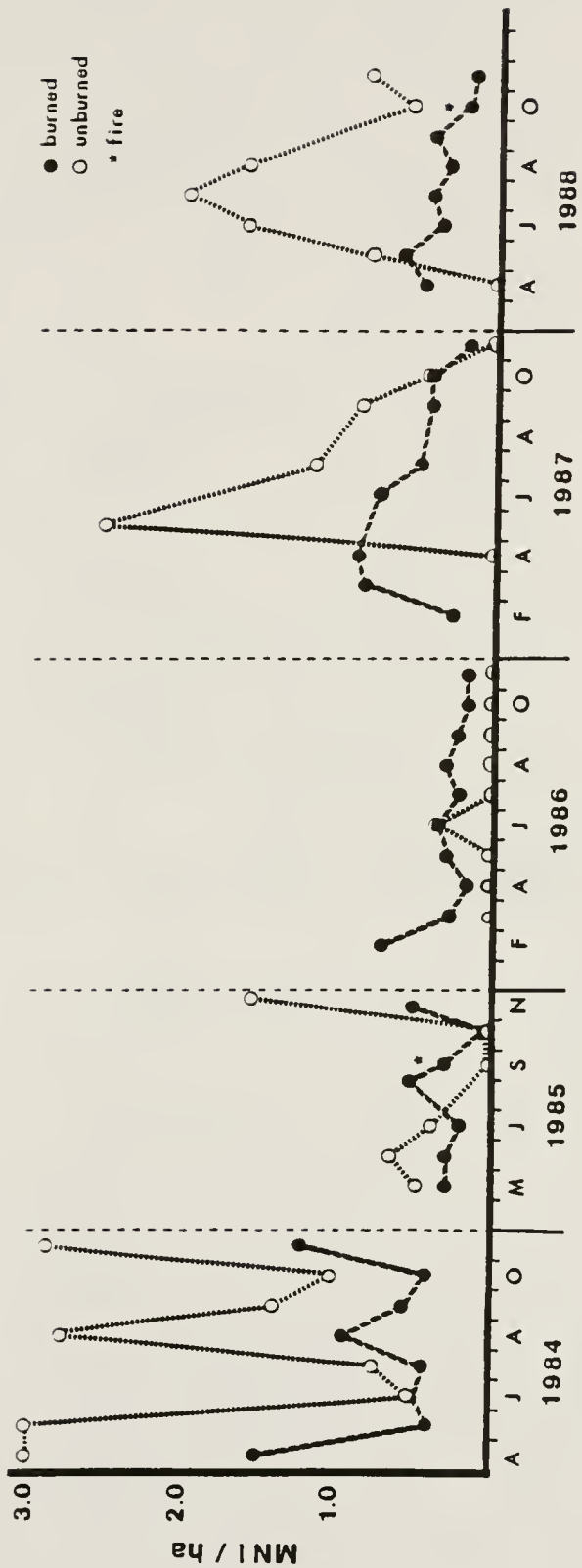

MNI / ha
3.0
2.0
1.0
burned
unburned
* fire
J
A
S
O
N
1987

Fig. 13. Apparent densities (expressed as minimum numbers of individual/ha) of Podomys on the burned and unburned areas of the Smith Lake Sandhill.


burned
unburned
fire
MNI / ha
3.0
2.0
1.0
A J A O
1984
M J S N
1985
F A J A O
1986
F A J A O
1987
A J A O
1988

two areas. During my fieldwork I noticed that all animals caught on the unburned sites (on all three sandhills) were captured at burrows on the periphery of the unburned area; none were captured in the middle of the unburned sites. For three months preceding and following the burns, trapping success on the three sandhills ranged from 2.2 to 8.4%; no significant differences before and after the fires were noted. On the unburned sites, trapping success ranged from 1 to 3.4%, the highest being on the BP ecotone.

Significantly more mice were caught in burned areas both before and immediately following a fire (Tables 14 and 15). Significantly more individuals were captured on burned sites (Table 16) than at unburned burrows ($G = 10.597$, significant at $p < 0.005$). The smaller difference in CIs between burned and unburned BP burrows was due presumably to the fact that all animals caught on the unburned area were captured at burrows on the periphery of the site with old pastures. There were numerous tortoise burrows, oaks, and open areas on this periphery. No animals were caught in the middle of the unburned area. The relatively smaller CI (11.84) for the burned burrows at BP was possibly due to differences in vegetation and past land use.

Prescribed burns appeared to have little or no immediate effects (i.e., three months following the burn) on Podomys populations. Some populations decreased but two or three months later populations equaled or exceeded pre-fire

TABLE 14. Burrows on burned sandhills. Data obtained from trapping Podomys at n burrows subjected to prescribed burns on the BP, LP, and SL sandhills. # is total number of individuals caught.

	Pre-burn	Post-burn
BP(n = 26)		
Trapnights	416	676
#	10	8[a]
Total captures	24	28
LP(n = 24)		
Trapnights	318	174
#	5	5[b]
Total captures	7	5
SL (n = 57)		
Trapnights	558	805
#	15	19[c]
Total captures	44	37

[a]includes 4 individuals captured before the burn.

[b]includes 2 individuals captured before the burn.

[c]includes 10 individuals captured before the burn.

TABLE 15. Burrows on unburned sandhills. Data obtained from trapping Podomys at n unburned burrows on the BP, LP, and SL sandhills. # represents number of individuals caught.

	BP	LP	SL
n	13	18	22
Trapnights	596	375	497
#	6	4	6
Total captures	24	6	9

TABLE 16. Comparison of capture indices for Podomys at burrows on burned and unburned sandhills (after Buech et al. (1977)). The burn/unburned column shows that the numbers of individuals captured in burned areas average 194% of those at unburned burrows.

	burn CI	unburned CI	burn/unburned %
BP	11.84	10.08	117%
LP	28.75	10.68	269%
SL	23.56	12.06	195%

levels (Figs. 11 and 13, Table 17). Bock and Bock (1983) suggested that fires in pine forest might increase the quantity or quality of food supplies, thus producing a temporary increase in the number of deer mice captured after a fire. Whether this is what happens on the sandhills is unknown. After the burns on my three sites, half of the mice captured after the fire (all adults) had not been caught before the fire; these animals might be dispersers from surrounding, unburned areas. Layne (1974) and Martell (1984) both suggested that burned areas might act as "dispersal sinks". Tevis (1956b), Hatchell (1964), Ahlgren (1966), Sims and Buckner (1973), and Krefting and Ahlgren (1974) documented dispersal of Peromyscus onto burned areas. Kaufman et al. (1988) suggested that odors from burned areas might stimulate immigration of P. maniculatus from suboptimal habitats.

To examine the effects of burns on home ranges, I arbitrarily selected animals who were captured at least five times, on the premise that two or three captures do not reveal significant information regarding size of home ranges. For the 13 animals thus qualified, activity areas did not significantly shift or change in size. At SL, the animals caught more than five times appeared to be concentrated on the periphery of the study area, near the xeric oak hammocks. Home ranges for eight animals on SL are shown on Fig. 14. The female (#70) captured in the middle of the

TABLE 17. Comparison of capture indices for Podomys at burrows on 3 burned sandhills (after Buech et al. (1977)).

	Pre-burn CI	Post-burn CI	Before/after (%)
BP	24.04	11.83	203%
LP	15.72	28.74	54.7%
SL	26.88	23.60	114%

Fig. 14. Home ranges of eight Podomys on the SL sandhill before (stippled) and after (hatched) the 1985 fire. Dots represent burrows where animals were captured; asterisk indicates burrow used by both males 32 and 39.

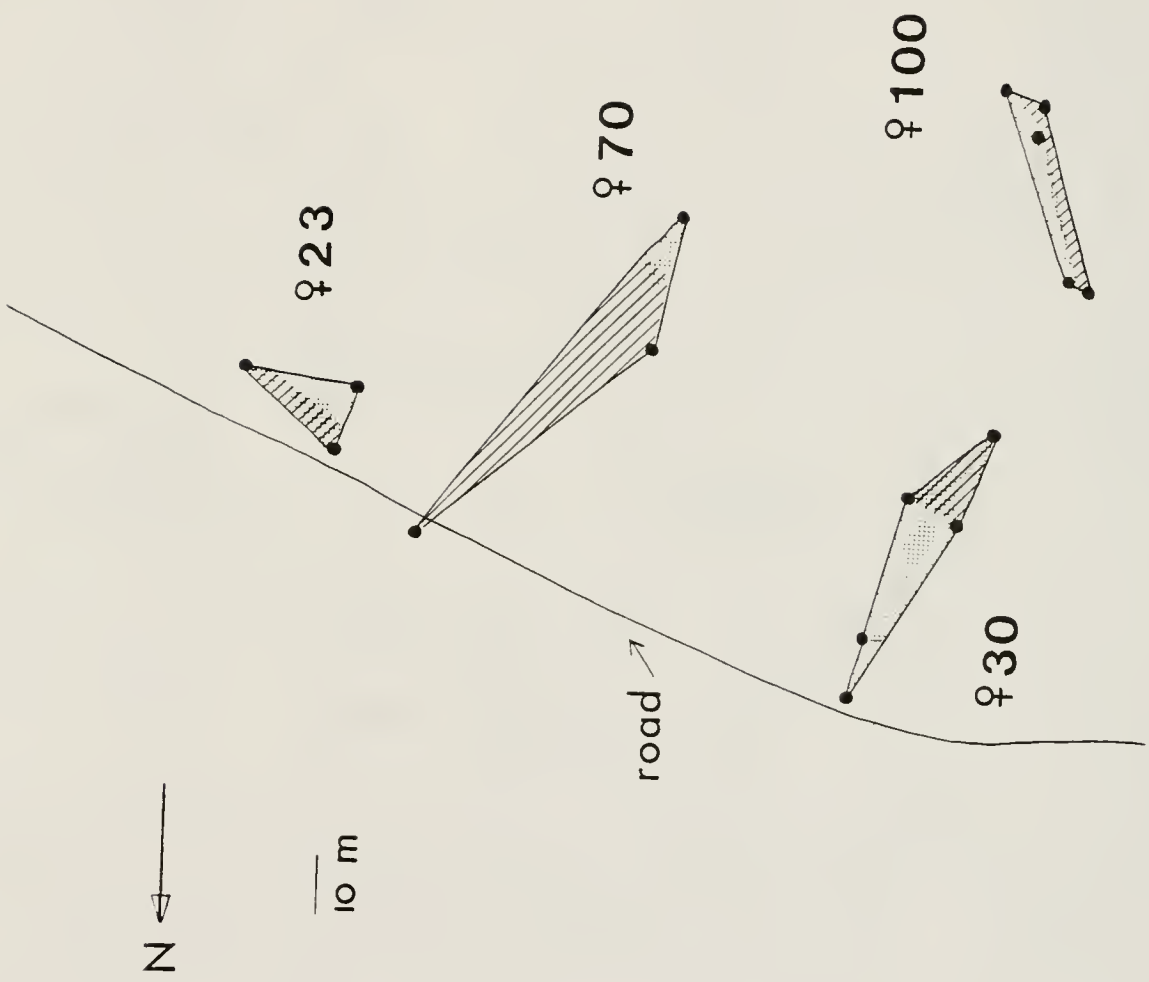
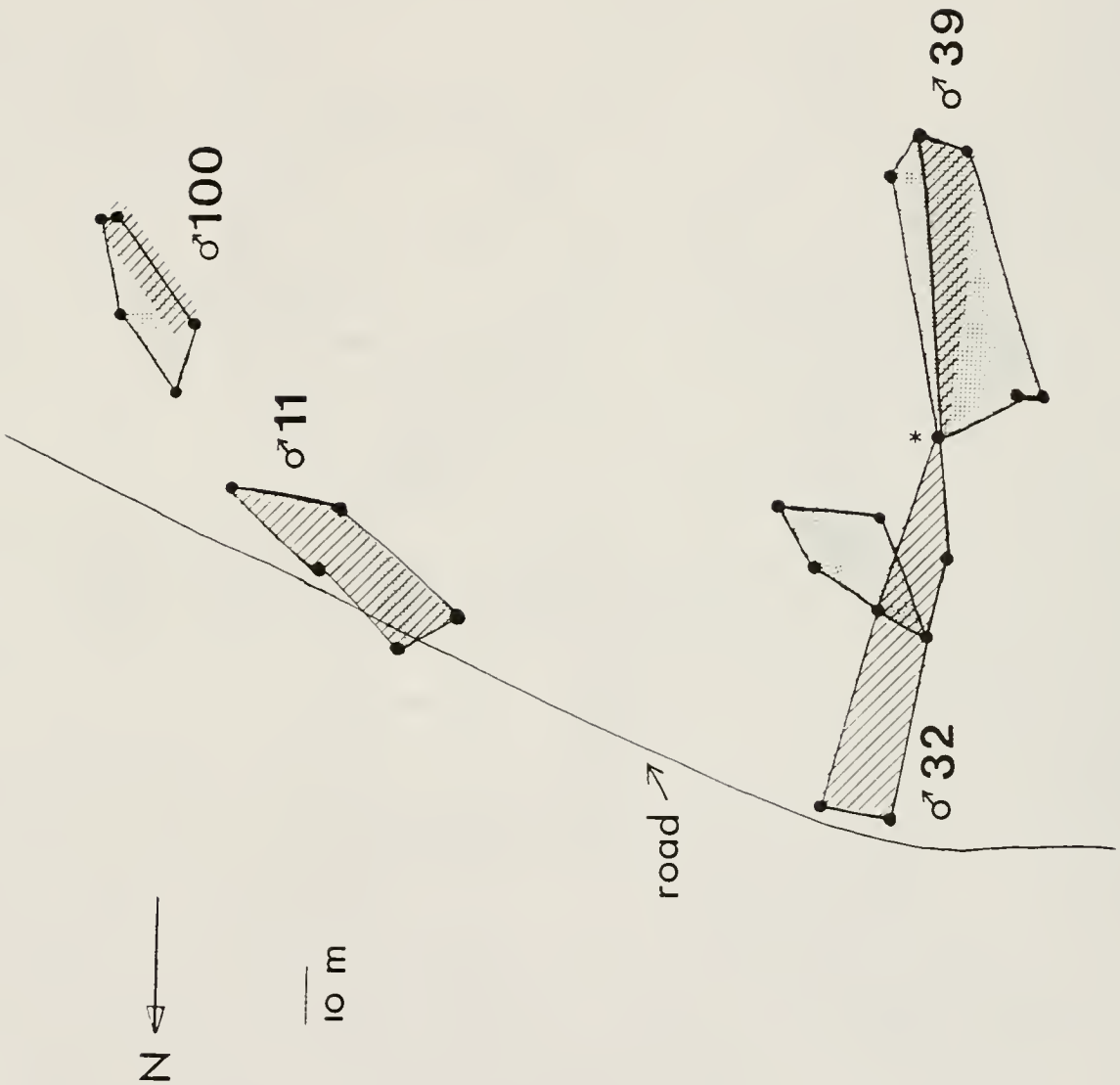

♀23
♀70
♀100
♀30
road
10 m
N

Fig. 14--continued


♂100
♂11
♂39
♂32
road
10 m
N

burned site crossed the road to the unburned area between 15 and 22 September; on 13 October, the date of her last capture, she had returned to a burrow on the burned side. This was my only observation of an animal moving from burned to unburned burrows after a fire, and she might have moved for reasons unrelated to the burn. For those animals that continued to be captured in 1986, no large shifts in activity area occurred. At BP, five mice were captured at least five times in the two months before and after the fire. Likewise, no major changes in activity areas were observed. At LP, no animals were captured more than three times; whether this indicated a larger home range or a faster turnover (due to death or dispersal) was unknown.

There is little or no mortality of Podomys directly attributable to fires on my study sites (Table 18), for two possible reasons. Because of the uneven distribution of litter and bare patches of sand, the effects of these fires occur in a mosaic of varying intensity. These are not catastrophic fires that burn or suffocate rodents, as occasionally observed in other habitats (Chew et al., 1959; Tevis, 1956b). Secondly, mice are protected by remaining within the tortoise burrows. Although logs, holes in trees, and burned out root channels are used as temporary shelters, as reported for Peromyscus by Baker (1974), Wolff and Hurlbutt (1982), and others, I have no evidence that my animals used long-term nests in logs or other structures above

TABLE 18. Survival of Podomys following three prescribed burns on the Ordway Preserve. N indicates the total number of mice captured during the month prior to fire; D indicates the percentage that disappeared during the month of the fire; A indicates the percentage alive during the month after the fire.

Site	N	D	A
BP	4	0	100
LP	3	0	100
SL	15	13	87

ground. Likewise, Layne (1970) considered Podomys to be exclusively burrow-dwelling.

I also compared trapping success on burned and unburned sites by examining trapping effort expressed as trapnights per total number of captures per hectare (Table 19); i.e., how much effort is required in an area before finding a mouse? No effort was made to make trapnights equivalent, but the total number of trapnights is listed for each year. Regardless of the number of trapnights, more time was needed to catch a mouse on the unburned sites. For all five years on the SL sites, the numbers of trapnights required to catch a mouse were much smaller and more consistent than on the unburned areas.

What is the effect of prescribed burns on young animals? From 1984 to 1988, I marked 17 young animals (juveniles and subadults) on the unburned side of SL and 81 young on the burn. I arbitrarily defined "resident" as an animal that was trapped at SL for more than six months and found that only 18 (10 females and 8 males) of those 98 young animals became residents on SL (Table 20). A higher percentage of the residents remained on the burned part of the sandhill: 3% of the juveniles and 9% of the subadults remained on the unburned side, and 15% of the juveniles and 11% of the subadults remained on the burn.

The Podomys population at SL reached its highest level in 1984 (Fig. 13) and persisted at lower numbers through

TABLE 19. Comparison of trapping effort on unburned and burned sandhills, where TN is the total number of trapnights and trapping effort is expressed as trapnight/capture/ha (TN/CAP/HA).

Unburned Site	Year	TN	TN/CAP/HA
BP	1988	830	19.53
LP	1987	371	51.53
SL	1984	476	7.39
	1985	784	14.74
	1986	786	280.71
	1987	429	15.32
	1988	704	8.38
Burned Site	**Year**	**TN**	**TN/CAP/HA**
BP	1988	1612	8.70
LP	1987	492	6.51
SL	1984	1444	0.64
	1985	2308	1.00
	1986	2958	1.17
	1987	1839	0.99
	1988	2789	1.02

TABLE 20. Residence of young Podomys on the SL sandhill, where N is the total number of young marked and R is the percentage of marked young that became residents on that sandhill.

	N	R
BURNED	81	26
NOT BURNED	17	12

1988. The decline did not appear to be due to fire, but might be related to food supply. For example, Kantola (1986) reported that turkey oaks on the Preserve produced many more acorns in 1983 than 1984. If acorns are a major food of Podomys, then failure of acorn crops might have a negative effect on mouse populations, although feeding experiments in high pine and sand pine scrub habitats have yet to show a positive response to supplemental food (Young and Stout, 1986 and Diet above). Populations at BP and LP were consistently lower than at SL.

Responses of Peromyscus to fires in a variety of habitats are listed in Table 21. Beck and Vogl (1972), Tester (1965), and Hedlund and Rickard (1981) noted that small mammals can survive fires by remaining in burrows. Most studies were short-term research on P. maniculatus, which showed a positive response to fires in almost all habitats. Population increases of Peromyscus have been correlated with changes in food, particularly seeds and insects (e.g., Tevis, 1956a; Ahlgren, 1966; Layne, 1974; Krefting and Ahlgren, 1974; Bock and Bock, 1983; Kaufman et al., 1983). The only evidence of qualitative differences in diets comes from Halford (1981), who showed that P. maniculatus on burns consumed fewer Lepidoptera and more Coleoptera and plant material than mice on unburned sites. Other authors related fluctuations of Peromyscus populations to changes in litter and other structural qualities of the environment (Tester

TABLE 21. Responses of *Peromyscus* species to fire. R = response (I = increase, D = decrease, 0 = no response) and Time is the duration of the study (in months).

State	Habitat	R	Time	Reference
P. californicus				
CA	mixed brush	D	30	Cook 1959
CA	chaparral	D	48	Lawrence 1966
P. gossypinus				
AL	longleaf pine	I	18	Boyer 1964
FL	slash & longleaf	I	36	Layne 1974[a]
LA	loblolly-shortleaf	I	~11	Shadowen 1963
LA	loblolly-shortleaf	I	varied among plots	Hatchell 1964
P. leucopus				
KS	tallgrass prairie	0	24	Kaufman et al. 1983
WI	brush prairie savanna	D	1	Beck & Vogl 1972
P. maniculatus				
AZ	ponderosa pine	I	~8	Lowe et al. 1978
CA	grassland	I	48	Lawrence 1966
CA	Douglas fir	I[b]	7	Tevis 1956a
CA	grassland	I	30	Cook 1959
	mixed brush	0	30	"
CA	mixed conifers & hardwoods	I	?	McDonald 1983

TABLE 21--continued

State	Habitat	R	Time	Reference
CO	lodgepole pine	I	3	Roppe & Hein 1978
ID	mixed conifers	I	1	Stout et al. 1971
ID	sagebrush	I[c]	7	Halford 1981
KS	tallgrass prairie	I	24	Kaufman et al. 1983; Peterson et al.1985
MN	jack pine	I	36	Ahlgren 1966
MN	mixed conifers & hardwoods	I[d]	144	Krefting & Ahlgren 1974
MN	jack pine & aspen-fir-spruce	D	2	Buech et al. 1977
MT	larch-Douglas fir	I	~60	Halvorson 1982
OH	oat monoculture	D	10	Crowner & Barrett 1979
OR	Douglas fir	I	132	Gashwiler 1970
OR	Douglas fir	I	21	Hooven & Black 1976
SD	ponderosa pine & pine savanna	I	24	Bock & Bock 1983
WI	brush prairie savanna	I	1	Beck & Vogl 1972
BRITISH COLUMBIA				
	mixed conifer	I	8	Sullivan 1980

TABLE 21--continued

State	Habitat	R	Time	Reference
MANITOBA				
	jack pine	I	36	Sims & Buckner 1973
ONTARIO				
	black spruce & mixed wood	I	~36	Martell 1984
P. polionotus				
AL	longleaf	I	18	Boyer 1964
FL	longleaf pine/ turkey oak	0	15	Arata 1959
GA	old field	I	6	Odum et al. 1973
P. truei				
CA	mixed brush	D	30	Cook 1959
CA	chaparral	D	48	Lawrence 1966
"*Peromyscus* spp."				
MN	oak/savanna (tallgrass prairie)	I	2	Tester 1965
PA	mixed oak	D[e]	15	Fala 1975

[a] 12 years later there was no significant difference in numbers on burned and unburned sites.

[b] Numbers were lower on uncut areas.

[c] Numbers increased after burn; there were, however, more animals on the control sites.

[d] Then decreased after 7 years.

[e] Numbers increased in the first month, then decreased.

1965; Beck and Vogl, 1972; Lowe et al., 1978; Blankenship, 1982). Martell (1984) reported that P. maniculatus on burns had significantly fewer botfly larvae than mice on clear-cuts. The success of P. maniculatus in particular on burned areas has been attributed to its preference for open areas and to increased food supplies (Peterson et al., 1985), possibly combined with an increase in the number of shelters provided by logs (Lowe et al., 1978). Competition with other species might be a factor in some communities. Halvorson (1982) studied P. maniculatus in larch-fir forest, where he suggested that deer mouse populations were affected by competition with Clethrionomys gapperi, but mice gained an advantage on open situations (e.g., burns) and in years when conifers produced large seed crops.

When fires in the high pine are suppressed, wiregrass might become more abundant but other herbaceous species decrease (Laessle, 1942; Hilmon and Hughes, 1965). On the Ordway Preserve, Gates and Tanner (1988) reported greater plant diversity on burned sandhills than on unburned controls, with greatest diversity occurring on sandhills burned within two years. At other sites, Hilmon and Hughes (1965) found greatest diversity three years after fire. They also suggested (1965:252) that "in central and southern Florida, however, where some growth occurs year-round, herbage stays green through the first winter after a fire; and sufficient rough to carry another fire accumulates only after two

years." Abrahamson and Abrahamson (1989) demonstrated that not all plants produce higher-quality fruit after fires even if vigorous sprouting occurs. Not enough is known about the diet of Podomys to determine whether fire affects populations of Florida mice through altering food supplies.

Conclusions

The prescribed burns on three high pine study sites on the Ordway Preserve did not have major impacts on mortality or the size and locations of home ranges of Podomys. In comparisons of burned and unburned sandhills, more trapping effort was required to capture animals on the unburned sites. Juveniles and subadults caught on the unburned sites are apparently dispersers; very few remain as residents on the unburned areas. Over a period of several years, numbers on the unburned sites were less predictable and less stable than on burned areas. On the unburned sites, I captured all mice at peripheral burrows (on the edge of the unburned sandhill near old pasture or burned sandhill habitats), and in some years I found no animals. Additional experiments with more replications (and burned and unburned sites of equal area) are needed, but these might be difficult to perform at Ordway, given the large home ranges and fluctuating populations of these animals.

The exact mechanism responsible for the effect of fire on Podomys was not determined. What is clear is that the

cessation of fire allows invasion of woody species into the high pine and a subsequent conversion to xeric hardwood or mixed pine forests (Laessle, 1958; Myers, 1985), in which Podomys are absent and species richness declines (Campbell and Christman, 1982; Humphrey et al., 1985; Brand, 1987; Gates and Tanner, 1988; Layne, in press). Although Peromyscus and other small mammals are abundant after fires in other habitats, it is tempting to speculate that the close association of the gopher mouse and gopher tortoise contributes to the success of Podomys in the sandhills. In fact, Gopherus and the species that utilize its burrows benefit indirectly from fire (Auffenberg and Franz, 1982; Jackson, 1985; Landers, 1987; Breininger et al., 1988). Fires serve to maintain an open canopy and stimulate new growth in plants that serve as forage for tortoises and possibly facilitate movement by hatchlings (Cox, Inkley, and Kautz, 1987).

Finally, I wish to emphasize how little is known about the effects of fires on small mammals. Before 1955, there was little interest in the effects of fire on small mammals (Taylor, 1981). Many of the early papers about fire and small, non-sciurid rodents reflect the forester's interest in rodents as predators of seeds and seedlings (e.g., Boyer, 1964; Ahlgren, 1966), and, as I have shown, many studies were of short duration. It is still rather surprising, however, that with the prevalence of both prescribed burns

and lightning strikes in the southeastern United States, that there is still so little research on effects on the non-game animals of the region. Between 1975 and 1979, only two papers were published regarding effects of fire on small mammals in the southeast (Taylor, 1981). Studies of long duration that examine seasonal effects of fire, costs of dispersal, and reactions of additional species are needed.

SUMMARY AND DISCUSSION

The purpose of this project was to examine the microhabitat use by P. floridanus in the high pine. I attempted to answer five questions:

1) Do Podomys in the high pine depend exclusively on tortoise burrows?

2) How large are home ranges?

3) Do dietary data explain why some tortoise burrows are preferred?

4) Is the local distribution of these mice predictable?

5) Do populations respond positively to burns?

To answer these questions, I monitored one population (SL) on the Ordway Preserve for five years. I also trapped on three additional sandhills (AC, BP, LP) for shorter periods of time and observed animals in a captive colony at the University of Florida.

Field workers at Ordway (Eisenberg, 1983; Brand, 1987; this study) have found Podomys to be generally restricted to high pine and old fields, where they are the only murid residents. Hammocks on the preserve are occupied by P. gossypinus and Ochrotomys nuttali, but Podomys might invade the edges of xeric hammocks in drought years, if tortoise burrows are available and if densities of the other murids

decrease. We suspect, but have not tested, that competitive exclusion occurs in most years and that Podomys is restricted to the high pine.

In my fieldwork I confirmed that, at least in the high pine on Ordway, Podomys reside exclusively in tortoise burrows. In more than 33,000 trapnights I observed mice entering holes of unknown origin only three times. Trap success at burrows (mean = 7% on SL) is higher than on grids (means = 0.5, 0.7, and 3.6% on three grids), as Eisenberg (1983) suggested. Florida mice certainly climbed plants and utilized fallen branches while foraging, but the typical escape response to trapping (at both grids and burrows) was to enter tortoise burrows. Mice modify burrows by constructing chimneys and U-shaped tunnels that open into the ceilings and sides of the main tortoise burrow. These structures probably served as escape routes from predators (presumably snakes) and they allowed occupation of burrows after tortoises left and the main entrances collapsed. I observed Podomys and Rana areolata simultaneously utilizing burrows, but interactions with other burrow residents are unknown. Florida mice probably are both predators and prey of other burrow commensals.

When trapping at burrows, I captured other burrow residents, particularly R. areolata. Although G. volans were captured at burrows 38 times (Table 1), there was no evidence that they actually resided in burrows. Other

rodents (P. gossypinus, S. hispidus, O. palustris) were found on the sandhills rarely, although they are known to utilize tortoise burrows (Jackson and Milstrey, 1989). The absence of other small rodents might be an indication that Ordway has harsher sandhills--more xeric with more unpredictable rainfall and food supplies--than those of other study sites. It would be interesting to compare population sizes and physical attributes of high pine sites on a state-wide basis.

At the SL burrows 255 individuals were marked between August 1983 and November 1988, 32% of which were captured only once. Mean trappability was 57%, with individual trappability ranging from 14 to 100%. As reported by Layne (1966) for populations in Alachua County, I found the majority of reproduction occurring between August and November. Juveniles could be marked outside what I believed to be natal burrows at approximately three weeks of age, judging by pelage and weight (9-14 g). Both pre- and post-reproductive dispersal appeared to occur, although I had no means of determining mortality. On the SL sandhill, 8.6% of all marked animals were present for 360 days or more; of these animals, half of the females were first marked as juveniles, whereas most of the males were marked as sub-adults or adults. The longevity records were 649 days for females and 920 days for males.

Almost nothing is known about the diet of Podomys, and studies of fecal or stomach contents are badly needed. In the field I observed mice eating insects, young shoots (Smilax), and Asimina fruits. Captive animals accepted a wide variety of acorns, pine seeds, and other fruits and flowers collected on Ordway, and cached favored foods. My preliminary tests of acorn preferences suggested that species other than Q. laevis might be preferred, but more strenuous tests need to be performed. Like that of Young and Stout (1986), my supplementation experiment did not have a positive effect on wild populations, suggesting that factors other than food determine local distributions of Podomys.

I examined home range size using three techniques: fluorescent powder, mark-and-release trapping at grids, and mark-and-release trapping at burrows. The first two techniques severely underestimated home range size. With the burrow data, I obtained mean annual home ranges of 2601 m^2 (SD = 1315.1) for 35 females and 4042 m^2 (SD = 2269.4) for 40 males, using the Exclusive Boundary Strip Method (Stickel, 1954; Davis, 1956). These means might be slightly underestimated, since some of these adults utilized edges of my study areas, but these figures were more realistic than those obtained on 100 m^2 grids. Home ranges of Podomys have not been reported previously, but based on the unpredictability of climate and food in the high pine, I would

predict home ranges in the scrub would be smaller. Adult females had mutually exclusive home ranges; this observation agreed with laboratory observations of litter mortality and aggressive behavior when unrelated females were housed together. Adult males had significantly larger home ranges, which overlapped with ranges of other adults.

Local distributions of Podomys were not solely dependent on numbers of tortoise burrows. For example, in their research on the Citrus Tract (Citrus and Hernando counties), Beckwith (1964) and Umber (1975) noted that Florida mice usually were captured on sandhills with native vegetation, rather than on sandhills converted to pine plantations, although tortoise density appeared to increase on the plantations. During the course of this study mice practically disappeared from AC, although plenty of tortoise burrows were still present. Clearly, distributions of Podomys cannot be predicted from burrow density alone.

On two sandhills (BP in 1988 and SL in 1985, 1987, and 1988) I sampled the vegetation in circular quadrats centered on 42 burrows to determine whether the presence of mice could be predicted on the basis of local plant structure or species composition. I found that the total number of captures was correlated ($p < 0.05$) with stem densities of turkey oak, longleaf pine, and persimmon, and with increased numbers of herbaceous species. Minimum numbers of individual mice could not be predicted as accurately. More

than 83% of the burrows sampled were reclassified correctly using the physical and vegetation parameters I measured (Table 13); i.e., the parameters I used were useful predictors of the relative abundance of Podomys at burrows.

Determining the response of Podomys to prescribed burns was more complicated than I expected. Five years of trapping might be too brief a period to determine population responses, and so far, most studies of fire and small mammals have been of even shorter duration. When I corrected for differences in area and trapping effort, I found that apparent densities on the unburned sites of the BP, LP, and SL sandhills frequently exceeded those on the burned sites. However--and this can be seen particularly with the SL data (Fig. 13)--apparent densities on unburned areas fluctuated more wildly and frequently reached zero. I interpreted my results as follows. In the short term, fires do not have a negative effect on Podomys, because I detected no mortality or movements of home ranges attributable to burns. In the long term, mice respond positively to fires, probably due to the larger numbers of tortoise burrows, increased diversity of herbaceous species, and the opening up of habitat. Total numbers of captures of mice at BP and SL were correlated with higher stem counts of longleaf pine (known to do best on burned areas), higher stem counts of turkey oak and persimmon (which produce extra shoots after fires), and herbaceous diversity (which, according to Gates and Tanner

(1988), reaches its maximum on Ordway sandhills two years after fire). On all of my study sites, we have not burned frequently enough to eradicate adult turkey oaks and persimmons, so these stem counts reflected coppicing due to fire and not numbers of large trees.

Several suggestions regarding management of P. floridanus on Ordway can be drawn from this study. First, a continuation of the present system of rotational burns (three-year cycles, different seasons) on the sandhills appears beneficial. Secondly, until we learn more of diet and interspecific interactions, maintaining a mosaic of sandhills and old fields would be a wise strategy. Conversion of SL to longleaf pine savanna or BP to turkey oak savanna might be detrimental to the species if diversity in plant composition is lost. Thirdly, protection and assessment of gopher tortoise populations should continue, under the assumption that whatever benefits Gopherus populations will benefit Podomys and other burrow residents as long as diversity in the high pine vegetation also is protected.

Although Podomys conserves water less well than Peromyscus and develops hypothermia at 10 C, it resides in tortoise burrows on the high sandhills of the preserve where Peromyscus does not. Podomys seems to be a good colonist in these areas and, as noted, its behavior differs from that of scrub populations. Podomys appears to be "k-selected" when compared to Peromyscus. Mace and Eisenberg (1982) noted the

large brain size relative to head and body weight; they associated relatively large brains with smaller litters, diet and habitat complexity, and larger numbers of sympatric congeners. This brain-body size relationship is consistent with earlier suggestions that the present distribution of Podomys is relictual.

APPENDIX

This is a list of plant species (excluding grasses and sedges) identified in vegetation samples around tortoise burrows at Blue Pond (BP) and Smith Lake (SL). Each species, and its frequency of occurrence in the high pine at Ordway (unless another habitat is noted), was identified using "Vascular Plants of the Ordway Preserve", compiled by David W. Hall and Richard Franz. The taxonomic arrangement of this list follows that of Wunderlin's "Guide to the vascular plants of central Florida" (1982). Voucher specimens were deposited in the Ordway Herbarium.

FAMILY PTERIDACEAE.
Pteridium aquilinum (L.) Kuhn. Bracken fern. SL. Abundant.

FAMILY PINACEAE.
Pinus clausa (Chapm. ex Engelm.) Vasey ex Sarg. Sand pine. SL. Scattered individuals.
Pinus elliotti Engelm. Slash pine. BP.
Pinus palustris Mill. Longleaf pine. BP,SL. Characteristic.
Pinus taeda L. Loblolly pine. BP. Characteristic in loblolly pine-bottomland hardwoods and some old fields.

FAMILY ARECACEAE.
Serenoa repens (Bartr.) Small. Saw palmetto. BP,SL. Occasional.

FAMILY COMMELINACEAE.
Commelina erecta L. Spreading dayflower. SL. Common.
Cuthbertia graminea Small. Roseling. BP,SL. Common.
Tradescantia roseolens Small. Scrub spiderwort. SL. Uncommon.

FAMILY SMILACACEAE.
Smilax auriculata Walt. Wild bamboo. BP,SL. Abundant in xeric live oak forests and ruderal sites.

FAMILY AGAVACEAE.
Yucca spp. Haw. Weak-leaf yucca. BP,SL. Common.

FAMILY MYRICACEAE.
Myrica cerifera L. Southern bayberry or wax myrtle. SL. Abundant.

FAMILY FAGACEAE.
Quercus chapmanii Sarg. Chapman's oak. SL. Common.
Quercus geminata Small. Sand live oak. BP,SL.
Quercus incana Bartr. Bluejack oak. BP,SL. Common.
Quercus laevis Walt. Turkey oak. BP,SL. Characteristic.
Quercus hemisphaerica Bartr. Laurel oak. BP,SL. Abundant on ruderal sites.
Quercus myrtifolia Willd. Myrtle oak. SL. Common in sand live oak hammocks.
Quercus stellata Wang. Small post oak. BP. Uncommon.
Quercus sp. L. Possible hybrid. BP.

FAMILY ARISTOLOCHIACEAE.
Aristolochia serpentaria L. Snakeroot. BP.

FAMILY POLYGONACEAE.
Eriogonum tomentosum Michx. Dog's tongue or wild buckwheat. BP,SL. Abundant.
Polygonella gracilis (Nutt.) Meisn. Wireweed. BP,SL. Abundant.

FAMILY CARYOPHYLLACEAE.
Paronychia patula Shinners. Spreading whittlow-wort. BP,SL.
Stipulicida setacea Michx. Wireweed. BP. Common.

FAMILY RANUNCULACEAE.
Clematis reticulata Walt. Vase-vine. BP,SL. Uncommon.

FAMILY ANNONACEAE.
Asimina incarna (Bartr.) Exell. Flag pawpaw. BP,SL. Abundant.
Asimina pygmaea (Bartr.) Dunal. Dwarf pawpaw. BP. Uncommon.

FAMILY CAPPARACEAE.
Polansia tenuifolia Torr. and Gray. Pineland catchfly. SL. Common.

FAMILY ROSACEAE.
Prunus serotina Ehrh. Wild cherry. SL. Uncommon on ruderal sites.

FAMILY CHRYSOBALANACEAE.
Licania michauxii Prance. Gopher-apple. SL. Abundant.

FAMILY FABACEAE.
Aeschynomene viscidula Michx. Prostrate jointvetch. BP,SL. Common in old fields.
Astragalus obcordatus Ell. SL. Uncommon.
Cassia chamaecrista L. Partridge pea. SL. Common.
Chapmannia floridana Torr. and Gray. Alicia. BP,SL. Abundant.
Clitoria mariana L. Butterfly-pea. BP,SL. Uncommon.

Crotalaria rotundifolia (Walt.) Gmel. Rabbit-bells. BP,SL. Common.
Dalea pinnata (Walt. ex Gmel.) Barneby. Summer farewell. BP. Common.
Desmodium strictum or D. tenuifolium Torr. and Gray. BP,SL. Common.
Desmodium viridiflorum (L.) DC. Velvet-leaved tick-trefoil. BP,SL. Common.
Erythrina herbacea L. Cherokee bean. SL. Common in hammocks.
Galactia regularis (L.) BSP. Prostrate milk-pea. BP,SL. Common.
Lespedeza hirta (L.) Hornem. Hairy bush-clover. SL.
Psoralea canescens Michx. Buckroot. BP,SL. Uncommon.
Rhynchosia cinerea Nash. Ashy Rhynchosia. BP.
Rhynchosia reniformis DC. Dollar-weed. BP,SL. Common.
Schrankia microphylla (Dry. ex Smith) Macbr. Smooth-leaved sensitive briar. BP,SL. Common.
Stylosanthes biflora (L.) BSP. Pencilflower. SL.
Tephrosia chrysophylla Pursh. Golden hoary-pea. BP,SL. Common.
Tephrosia florida (Dietr.) Wood. Long-stalked hoary-pea. BP.
Tephrosia spicata? (Walt.) Torr. and Gray. Sand pea. SL. Common in old fields.
Tephrosia virginiana (L.) Pers. Goat's rue. BP,SL. Abundant.

FAMILY POLYGALACEAE.
Polygala grandiflora Walt. Large-flowered polygala. SL. Uncommon.

FAMILY KRAMERIACEAE.
Krameria lanceolata Torr. Sandbur. SL. Abundant.

FAMILY EUPHORBIACEAE.
Chamaesyce cordifolia (Ell.) Small. Round-leaved spurge. BP.
Cnidoscolus stimulosus (Michx.) Engelm. and Gray. Bull-nettle. BP,SL. Abundant.
Croton argyranthemus Michx. Silver croton. BP,SL. Abundant.
Croton glandulosus L. Tropic croton. SL.
Stillingia sylvatica L. Queen's delight. BP,SL. Common.
Tragia urens L. Eastern tragia. BP,SL. Common on old fields.

FAMILY EMPETRACEAE.
Ceratiola ericoides Michx. Florida rosemary. SL. Occasional.

FAMILY ANACARDIACEAE.
Rhus copallina L. Winged sumac. BP,SL. Abundant.

FAMILY VITACEAE.
Vitis aestivalis Michx. Summer grape. BP,SL. Common on old home sites.

FAMILY HYPERICACEAE.
Hypericum hypericoides (L.) Crantz. St. Andrew's-cross. SL. Common.

FAMILY CISTACEAE.
Lechea patula Legg. Narrow-leaved pinweed. SL.
Lechea sp. L. Pinweed. BP,SL.

FAMILY VIOLACEAE.
Viola septemloba LeConte. Seven-lobed violet. SL. Uncommon.

FAMILY TURNERACEAE.
Piriqueta caroliniana (Walt.) Urban. Smooth stem piriqueta. BP,SL. Common.

FAMILY CACTACEAE.
Opuntia humifusa (Raf.) Raf. Prickly-pear cactus. BP,SL. Common.

FAMILY APIACEAE.
Eryngium aromaticum Baldw. ex Ell. Fragrant eryngium. BP,SL. Common.

FAMILY ERICACEAE.
Vaccinium arboreum Marsh. Sparkleberry. BP,SL. Occasional.
Vaccinium corymbosum L. Highbush blueberry. SL. Common in mesic hardwood hammocks.
Vaccinium myrsinites Lam. Shiny blueberry. BP,SL. Common.
Vaccinium stamineum L. Deerberry. SL. Common.

FAMILY EBENACEAE.
Diospyros virginiana L. Persimmon. BP,SL. Abundant.

FAMILY APOCYNACEAE.
Amsonia ciliata Walt. Bluestar. BP,SL. Abundant.

FAMILY ASCLEPIADACEAE.
Asclepias humistrata Walt. Sandhill milkweed. BP,SL. Common.
Asclepias tuberosa subsp. rolfsii (Britt.) Woods. Fiddleleaf butterfly-weed. BP. Uncommon.
Asclepias verticillata L. Whorled-leaf milkweed. BP,SL. Uncommon.

FAMILY CONVOLVULACEAE.
Stylisma patens (Desr.) Myint. Trailing stylisma. BP,SL. Common.

FAMILY POLEMONIACEAE.
Phlox nivalis Lodd. Trailing phlox. SL. Uncommon.

FAMILY VERBENACEAE.
Callicarpa americana L. American beauty-berry. SL. Common.
Stylodon carneus (Medic.) Mold. SL.

FAMILY LAMIACEAE.
Salvia azurea Lam. Blue sage. BP. Uncommon.
Scutellaria multiglandulosa (Kearney) Small. Rolled-leaf skullcap. SL. Common.

FAMILY SCROPHULARIACEAE.
Linaria floridana Chapm. Florida toadflax. SL. Common.
Seymeria pectinata Pursh. Sticky seymeria. BP,SL. Common.

FAMILY ACANTHACEAE.
Dyschoriste oblongifolia (Michx.) Kuntze. Twin flower. SL. Common.

FAMILY RUBIACEAE.
Galium pilosum Ait. Bedstraw. BP.
Hedyotis procumbens (Gmel.) Fosberg. Fairy footprints. BP,SL. Common.

FAMILY ASTERACEAE.
Arnoglossum floridanum (A. Gray) H. Robins. Indian-plantain. SL.
Aster tortifolius Michx. White-topped aster. BP,SL. Locally common.
Balduina angustifolia (Pursh) Robins. Yellow buttons. BP,SL. Common.
Berlandiera subacaulis (Nutt.) Nutt. Common greeneyes. BP,SL. Abundant.
Carphephorus corymbosus (Nutt.) Torr. and Gray. Large-headed carphephorus. BP,SL. Abundant.
Cirsium sp. Mill. SL.
Conyza canadensis (L.) Cronq. Dwarf horseweed. BP.
Elephantopus elatus Bertol. Florida elephant's foot. BP,SL. Abundant.
Eupatorium compositifolium Walt. Dog fennel. BP,SL. Abundant.
Eupatorium jucundum Greene. Ageratina. BP,SL. Abundant.
Euthamia tenuifolia (Michx.) Greene. Flat-topped goldenrod. BP. Uncommon.
Helianthus angustifolius L. Narrow-leaved sunflower. BP.
Hieracium megacephalon Nash. Large-headed hawkweed. SL. Common.
Hieracium sp. L. Hawkweed. SL.
Liatris pauciflora Pursh. Lopsided blazing-star. BP,SL. Abundant.

Liatris tenuifolia Nutt. Fine-leaf blazing-star. BP,SL. Abundant.
Phoebanthus grandiflora (Torr. and Gray) Blake. BP,SL. Uncommon.
Pityopsis graminifolia (Michx.) Nutt. Silk-grass. BP,SL. Abundant.
Pterocaulon pycnostachyum (Michx.) Ell. Blackroot. SL. Uncommon.
Pyrrhopappus carolinianus (Walt.) DC. False dandelion. BP,SL. Uncommon.
Rudbeckia hirta L. Black-eyed susan. BP. Common on roadsides and old fields.
Silphium compositum Michx. Rosin weed. BP,SL. Common.
Solidago chapmanii Torr. and Gray. Chapman's goldenrod. BP. Common.
Verbesina heterophylla (Chapm.) Gray. Crownbeard. BP. Rare.

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BIOGRAPHICAL SKETCH

Cheri Jones was born in Albuquerque, New Mexico, on December 1, 1957, one of two children to Charlene and Clyde Jones. As the family of a mammalogist, the Joneses lived in Louisiana, Virginia, Colorado, Texas, and Equatorial Guinea, West Africa. At various times over the years her parents maintained bats in the basement, hyraxes in the bathroom, hamsters in the den, and monkeys in the family room. It is hardly surprising that both offspring developed environmental interests and scientific careers.

She earned her B.A. in 1979 from the Department of Biology at Hastings College and her M.S. in biology in 1982 from Fort Hays State University. While attending the University of Florida, she was a member of the Florida Committee on Rare and Endangered Plants and Animals, spent a semester in Costa Rica, and served as an officer for the U.F. chapter of Graduate Assistants United. Her professional affiliations include the American Association for the Advancement of Science, American Institute of Biological Sciences, American Society of Mammalogists, Florida Academy of Sciences, Gopher Tortoise Council, North Dakota Natural Science Society, Organization for Tropical Studies,

Southwestern Association of Naturalists, Sigma Xi, and the Wildlife Society.

I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.

John F. Eisenberg, Chairman
Katharine Ordway Professor of
Ecosystem Conservation

I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.

John H. Kaufmann
Professor of Zoology

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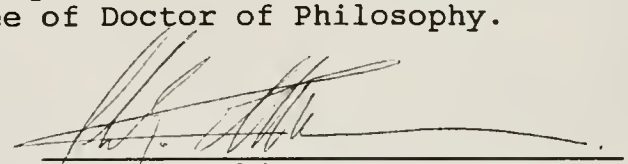
Richard A. Kiltie
Associate Professor of Zoology

I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.

Francis E. Putz
Associate Professor of Botany

I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.



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This dissertation was submitted to the Graduate Faculty of the Department of Zoology in the College of Liberal Arts and Sciences and to the Graduate School and was accepted as partial fulfillment of the requirements for the degree of Doctor of Philosophy.

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